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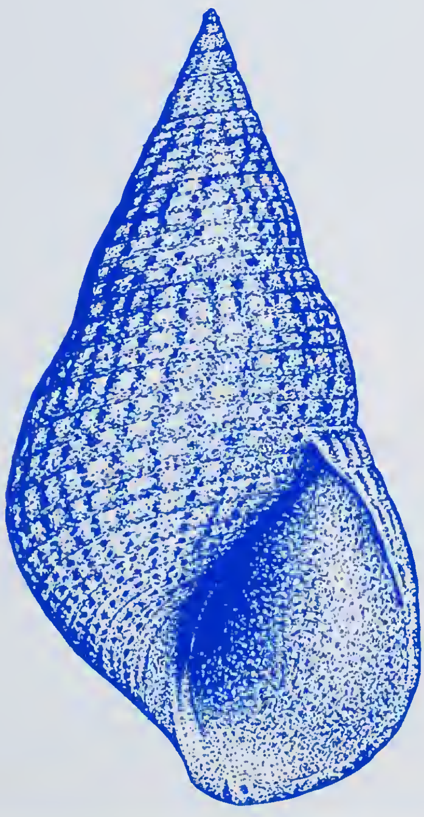

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Records
of the
Western Australian Museum

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Cover: *Littoraria melanostoma*, a mangrove snail that is widespread in the Indo-West Pacific.
Illustration by Jill Ruse.

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The water mite genus *Koenikea* Wolcott from Australia (Acari: Hydrachnidia: Unionicolidae)

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Abstract – Six new *Koenikea* species are described, *viz. K. circularis, K. gracilipalpis, K. lewisensis, K. pauciacetabulata, K. rubipes* and *K. setosa*. *Koenikea verrucosa* Lundblad is synonymized with *K. australica* Lundblad, and *K. purpurea* Smit with *K. crinita* Cook. New descriptions are provided for the female of *K. curtiseta* Cook and also for what is very likely the female of *K. jacunda* Cook, and for males of *Koenikea distans* K.O. Viets and *K. lemba* Cook. The genus is reported for the first time from Western Australia, the Northern Territory and South Australia. Finally, a key is given for all known Australian species.

INTRODUCTION

Koenikea species are among the most common water mite genera occurring in standing water in Australia (personal observation). The genus is also found in rivers, mainly in parts with reduced flow. So far, 17 species have been described from Australia (Harvey, 1998). Worldwide many subgenera have been described, but from Australia only two subgenera are known, i.e. *Koenikea* and *Notomideopsis*. Within Australia, there are no published records of *Koenikea* from South Australia, Western Australia and the Northern Territory (Harvey, 1998).

Outside Australia, *Koenikea* is widely distributed. The genus is known from Africa, while numerous species have been described from South America (Lundblad, 1943). In the New World *Koenikea* occurs as far north as Canada (Cook, 1974). Within the Australian faunal region, *Koenikea* species are known from New Guinea (Wiles, 1997) and New Caledonia (Smit, 2002), and they have also been found in Fiji (Smit, 2003).

In Australia, quite a few species are known from a few specimens only or from a limited geographical area. Therefore, variation in measurements or characters is poorly known.

The results presented in this study are from collection trips to all states of Australia, including the Northern Territory. In this paper, two species are synonymized, and a description is given of six new species, bringing the total number of species known from Australia to 21. A first description is given for the female of *K. curtiseta* Cook and very likely a first desciption is given for *K. jacunda* Cook, and for males of *Koenikea distans* K.O. Viets and *K. lemba* Cook. A key is given for all known Australian species.

MATERIAL AND METHODS

Unless stated otherwise, all material has been collected by the author. All non-type material has been deposited in the Zoological Museum of the University of Amsterdam (ZMAN) and the Western Australian Museum in Perth (WAM).

The following abbreviations have been used: PI-PV palp segments 1-5; IV-leg-4-6 fourth-sixth segments of fourth leg; d.s. dorsal shield; dgl dorsoglandularia; cxgl coxoglandularia; SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; NMV Museum of Victoria, Melbourne; NTM Museum and Art Gallery of the Northern Territory; SAM South Australian Museum, Adelaide; QM Queensland Museum, Brisbane.

Range measurements given comprise all specimens mentioned in the material examined. All *Koenikea* species have ventral and dorsal shields, and this is not repeated in the descriptions of the new species. Frequently the minute setae associated with the glandularia are lost (e.g. as a result of mounting), and consequently, they are not illustrated.

SYSTEMATICS

Koenikea Wolcott

Koenikea Wolcott, 1900: 189.

Koenikea (Koenikea) sorpresa Cook

Koenikea (Koenikea) sorpresa Cook, 1986: 199; Smit, 1992: 103; Harvey, 1998: 142.

Material Examined

Paratype

Female, Nigger Creek, south of Herberton, Queensland, Australia, 4 May 1981, leg. D.R. Cook (NMV K578).

Other material

Australia: Western Australia: 1 female, small pond near Crossing Pool, Millstream-Chichester National Park, 16 August 1994; 3 males, Fortescue River at crossing with highway, 18 August 1994; 1 female, Cockatoo Creek at crossing with Great Northern Highway, 8 September 1998; 1 female, Fitzroy River at crossing with Great Northern Highway, south of Derby, 8 September 1998; 4 females, plunge pool Adcock Gorge, Kimberley, 12 September 1998; 1 male, 3 females, pond Kalamina Gorge (near falls), Hamersley Range National Park, 13 August 1994 (WAM); 2 females, pond near Adcock Gorge, Kimberley, 12 September 1998; 2 males, 3 females, pool Amalia Gorge, El Questro Station, Kimberley, 16 September 1998; 1 male, 1 female, Spillway Creek, near Lake Argyle, 20 September 1998 (WAM); 1 female, Palm Springs, south of Halls Creek, 25 September 1998; 1 female, unnamed creek at crossing with Windjana Gorge Road, 38 km north of Great Northern Highway, Kimberley, 30 September 1998 (WAM). **Northern Territory**: 1 female, Radon Springs, Kakadu National Park, 19 July 1994; 17 males, 24 females, Lake Jabiru, Jabiru, 20 July 1994; 2 males, 1 female, pond in Jim Jim Creek, near Jim Jim Campground, Kakadu National Park, 23 July 1994; 3 females, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 2 females, Lily Pond Falls, Katherine Gorge National Park, 27 July 1994. **Victoria**: 2 females, Shipwreck Creek, Mallacoota, Croajingolong National Park, 23 October 1997. **Queensland**: 3 females, Nankeen Creek, 4 May 1981, leg. A.P. Mackay; 1 female, same location, 26 June 1982; 1 female, Fitzroy River, Rockhampton, 13 April 1983, leg. A.P. Mackay.

Remarks

The original description of the species was based on three specimens only. Therefore, some additional measurements are given here. Males of this study are 429–551 µm long and 425–575 µm wide. Females exhibit a large variation in size, and were 494–721 µm long and 478–729 µm wide. Moreover, there is much variation in the shape. Length/width ratio varies from 0.99–1.15 in the females and 1.04–1.08 in the males. The coxal setae of my specimens are much longer than illustrated by Cook (1986). I examined one of the paratype females, but most of these setae have been lost or are not well visible. Previously reported from Queensland and New South Wales, *K. sorpresa* is reported here for the first time from Victoria, the Northern Territory and Western Australia.

Koenikea (Notomideopsis) australica Lundblad

Koenikea (Koenikea) australica Lundblad, 1941: 117; Lundblad, 1947: 63; Cook, 1986: 185; Smit, 1992: 103; Harvey, 1998: 142.

Koenikea (Koenikea) verrucosa Lundblad, 1947: Cook, 1986: 185; 65; Smit, 1992: 103; Harvey, 1998: 142. **New syn.**

Material Examined

Australia: Tasmania: 1 male, Apsley River at crossing with Tasmania Highway, 19 October 1997; 7 males, 21 females, Jock's Lagoon, south of St Helens, 20 October 1997; 1 female, Windmill Lagoon, St Helens, 20 October 1997; 9 males, 47 females, 2 nymphs, swamp 12 km south of Gladstone, along road B82, 20 October 1997; 3 females, Big Waterhouse Lake, Waterhouse Protected Area, 21 October 1997. **Western Australia**: 2 females, 1 nymph, Moore River, at crossing with Brandt's Highway, Regans Ford, 26 August 1994. **Victoria**: 2 males, 14 females, Shipwreck Creek, Mallacoota, Croajingolong National Park, 23 October 1997; 4 males, 11 females, unnamed creek 4.5 km east of Shipwreck Creek, Croajingolong National Park, 23 October 1997; 3 females, Darby River, Wilsons Promontory National Park, 27 October 1997.

Remarks

Lundblad (1947) based his description of *K. verrucosa* on two males. Males show large variation in the size of the tubercles. Therefore, contrary to my earlier opinion (Smit, 1992), I now agree with Cook (1986) that the two species are conspecific.

Females show quite a bit of variation in size. Specimens from one location from Tasmania vary in length between 721 µm and 925 µm, in width between 591 µm and 838 µm.

Widespread in eastern Australia, previously reported from Tasmania, Victoria, New South Wales and Queensland. The species is reported here for the first time from Western Australia.

Koenikea (Notomideopsis) branacha Cook

Koenikea (Notomideopsis) branacha Cook, 1986: 190; Smit, 1992: 103; Harvey, 1998: 142.

Material Examined

Type material: Holotype male, creek on Bunya

Mt. road, 6 km south of Bunya Highway, Queensland, 23 April 1981, leg. D.R. Cook (NMV K564). Paratype female, same data as holotype (NMV K565).

Other material

Australia: Western Australia: 1 female, pond Kalamina Gorge (near falls), Hamersley Range National Park, 13 August 1994; 1 female, Chinderwariner Pool, Millstream-Chichester National Park, 15 August 1994; 4 females, western part Deep Reach Pool, Millstream-Chichester National Park, 16 August 1994; 8 females, 1 male, Crossing Pool, Millstream-Chichester National Park, 16 August 1994 (WAM); 1 female, Fortescue River at crossing with highway, 18 August 1994; 1 male, 11 females, Cockatoo Creek at crossing with Great Northern Highway, 8 September 1998; 1 female, pool Lennard River, Windjana Gorge National Park, 9 September 1998; 4 females, pools 3 km from Lennard Gorge, Kimberley, 10 September 1998; 1 female, pool downstream of Manning Gorge Falls (at campground), Kimberley, 12 September 1998; 1 female, pool near Adcock Gorge, Kimberley, Western Australia, 12 September 1998; 14 females, plunge pool Adcock Gorge, Kimberley, 12 September 1998 (WAM); 2 females, pool Galvans Gorge, Kimberley, 12 September 1998; 2 females, pool Manning Gorge Falls, Kimberley, 13 September 1998; 1 female, Russ Creek at crossing with Gibb River Road, Kimberley, 14 September 1998; 12 females, Miner's Pool, Drysdale River Homestead, Kimberley, 14 September 1998 (WAM); 1 male, 15 females, pool Amalia Gorge, El Questro Station, Kimberley, 16 September 1998; 9 females, Zebedee Springs (hot springs), El Questro Station, Kimberley, 16 September 1998; 6 females, Middle Springs, west of Kununurra, 18 September1998 (WAM); 4 males, 48 females, pool Valentine Springs, west of Kununurra, 18 September 1998; 4 females, Lake Kununurra, 10 km southeast of Kununurra, 19 September 1998; 5 females, Spillway Creek, near Lake Argyle, 20 September 1998; 1 male, 6 females, pool Saw Pit Gorge, south of Halls Creek, 25 September 1998 (WAM); 1 female, pools in creek at Old Halls Creek, south of Halls Creek, 26 September 1998; 1 female, pool west of Tunnel Creek, Tunnel Creek National Park, Kimberley, 30 September 1998. **Queensland**: 1 female, Fitzroy River, Yaamba, 30 May 1982, leg. A.P. Mackay; 3 females, Fitzroy River, Rockhampton, 23 November 1982, leg. A.P. Mackay; 1 female, same location, 4 January 1983; 2 females, same location, 1 March 1983; 1 female, same location, 15 March 1983; 3 females, same location, 13 April 1983; 4 females, same location, 30 August 1983; 1 female, same location, 8 November 1983; 1 male, 3 females, same location, 6 December 1983; 1 female, same location, 20 February 1984; 1 female, same location, 5 March 1984; 2 females, Catfish Waterhole, Lakefield National Park, 4 September 2000; 1 female, West Claudie River, Iron Range National Park, 7 September 2000; 1 male, Packers Creek, Iron Range National Park, 9 September 2000; 1 male, 3 females, Cockatoo Creek, Cape York Peninsula, 11 September 2000; 1 female, Coen River at Coen, 12 September 2000; 1 female, Broken River near Conical Pool, Eungella National Park, 18 September 2000; 1 male, 23 females, Little Yabba Creek, south of Kenilworth, 20 September 2000. **Northern Territory**: 1 female, Magela Creek floodplain, Island Billabong, 22 January 1979, leg. R. Tait (SMF 7162); 1 male, 3 October 1979, same location, leg. R. Tait (SMF 7147); 1 female, Magela Creek floodplain, Nankeen Billabong, 4 October 1979, leg R. Tait (SMF 7119); 7 males, 8 females, Radon Springs, Kakadu National Park, 19 July 1994; 2 males, Home Billabong, Kakadu National Park, 22 July 1994; 1 male, 2 females, plunge pool Gunlom Falls, Kakadu National Park, 25 July 1994; 3 males, 4 females, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 1 male, 3 females, Lily Pond Falls, Katherine Gorge National Park, 27 July 1994; 1 male, Katherine river near visitors centre, Katherine River National Park, 28 July 1994; 1 male, 1 female, pond Chinaman Creek, 16 km south of Katherine, 29 July 1994; 1 female, plunge pool Edith Falls, Katherine Gorge National Park, 30 July 1994; 1 female, outlet Upper Pool, Edith Falls, Katherine Gorge National Park, 30 July 1994; 1 male, billabong near Douglas Hot Springs, 1 August 1994; 1 male, Manton Dam, 1 August 1994. **South Australia**: 1 female, Dalhousie Springs, spring Ca5, 14 June 1984, leg. W. Zeidler & K.L. Gowlett (SAM).

Morphology

Male

Body 462–535 µm long and 458–502 µm wide. Genital field bulging. IV-leg-6 with 4-5 setae on ventral margin.

Female

Body 518–745 µm long and 478–648 µm (745 µm) wide. Genital field bulging. IV-leg-6 with six setae on ventral margin.

Remarks

Morphologically, *Koenikea branacha* is in all aspects similar to *K. distans* K.O. Viets. Also the females are very close to those of *K. pseudodistans* Cook. Cook (1986) separated *K. branacha* and *K. distans* based on the shape of the body, but in my opinion this is not a good character. *Koenikea branacha* is much smaller, and leg and palp segments are shorter (see Table 1). The body length of the male of *K. branacha* is smaller than 550 µm, while the female of *K. branacha* is smaller than 700 µm (but occasionally up to 745 µm).

Table 1 Measurements of females of *Koenikea branacha* and *K. distans*.

slide species	K565 *branacha* Paratype	AUS245 *branacha* –	AUS247 *branacha* –	AUS248 *branacha* –	AUS244 *distans* –	6724 *distans* Holotype	6450 *distans* –
L	656	559	616	616	–	826	770
W	608	535	573	599	–	798	–
d.s. L	619	518	559	559	786	761	705
d.s. W	502	446	510	526	688	688	624
PI	22	17	20	14	26	26	18
PII	82	78	68	74	106	96	82
PIII	42	40	38	38	56	48	46
PIV	82	75	70	80	108	96	82
PV	38	32	32	30	44	38	36
I-leg-4	158	154	158	169	234	200	172
I-leg-5	148	127	150	152	206	184	164
I-leg-6	158	126	120	130	194	178	160
IV-leg-4	163	145	154	162	220	200	190
IV-leg-5	190	160	188	200	266	228	214
IV-leg-6	170	152	172	176	246	200	190

IV-leg-6 of the female is shorter than 170 µm in *K.branacha*, and longer than 190 µm in *K. distans*. In the males IV-leg-6 is shorter than 181 µm in *K. branacha*, and longer than 206 µm in *K. distans*. In his key, Cook (1986) separated *K. branacha* from *K. pseudodistans* by using the size of the gland openings, but the only reliable character is the size of the claws of the fourth legs, which are enlarged in *K. pseudodistans* (see under the latter in this paper).

Previously, the species has been reported from New South Wales and Queensland, and it is reported here for the first time from Western Australia, the Northern Territory and South Australia.

Koenikea (Notomideopsis) circularis sp. nov.
Figures 1–7

Material Examined

Holotype

Female, stream El Questro Gorge, El Questro Station, Kimberley, Western Australia, Australia, 15 September 1998 (WAM).

Paratypes

Female, same data as holotype (ZMAN); 1 male, plunge pool Adcock Gorge, Kimberley, Western Australia, 12 September 1998 (WAM); 1 female, pool Manning Gorge Falls, Kimberley, 13 September 1998 (ZMAN); 1 male, 1 female, 17 Mile Creek, tributary of Katherine River, Katherine Gorge National Park, Northern Territory, Australia, 28 July 1994 (NTM).

Diagnosis

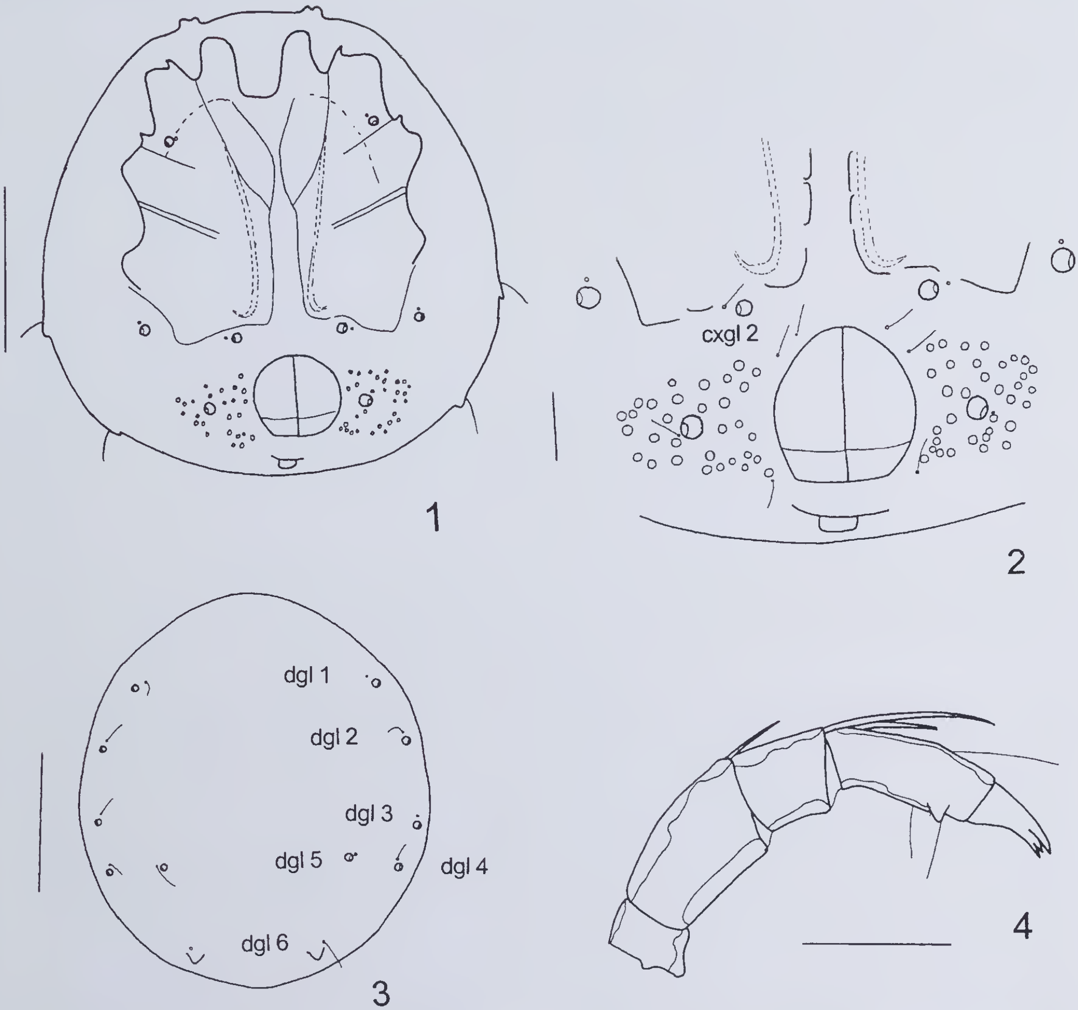
Apodemes very long, extending to posterior margin of fourth coxal plates.

Description

Male

Body 591 µm (526 µm) long and 591 µm (526 µm) wide. Dorsal shield 551 µm long and 551 µm wide. Dorsal shield with six pairs of glandularia; glandularia 3, 4 and 6 on small tubercles. First coxal plates not extending to anterior body margin. Apodemes of anterior coxal plates very long, extending almost to posterior margin of fourth coxal plates. Coxoglandularia 2 located near posterior margin of fourth coxal plates. Gonopore 74 µm long. Genital plates with approximately 20–25 acetabula, which are surrounding an enlarged glandularium. Lengths of PI-PV: 18 µm, 58 µm, 38 µm, 60 µm, 26 µm; peg-like seta of PIV on a short tubercle. Lengths of I-leg-4-6: 104 µm, 108 µm, 118 µm. Grooved or fluted setae ("rillborsten") of first and second legs relatively short. Lengths of IV-leg-4-6: 151 µm, 160 µm, 172 µm; chaetotaxy of IV-leg-5 and -6 as in female. I-leg-5 and II-leg-5 with two swimming setae, III-leg-4 with two and III-leg-5 with three swimming setae, IV-leg-3 with one, IV-leg-4 with five and IV-leg-5 with three swimming setae.

Female: body 557 µm (582–640 µm) long and 559 µm (575–632 µm) wide. Dorsal shield 502 µm long and 506 µm wide. Dorsal shield with six pairs of glandularia, glandularia 4 and 5 lying in a line. Glandularia 6 on small tubercles. First coxal plates not extending to anterior body margin. Apodemes of anterior coxal plates very long, extending almost to posterior margin of fourth coxal plates. Coxoglandularia 2 located near posterior margin of fourth coxal plates. Gonopore 108 µm long. Genital plates with approximately 30 acetabula, which are surrounding an enlarged glandularium. Lengths of PI-PV: 18 µm, 58 µm, 34 µm, 58 µm, 31 µm. Peg-like seta of PIV not on a tubercle. Lengths of I-leg-4-6: 90 µm, 90 µm, 80 µm. Rillborsten of first and second leg



Figures 1–4 *Koenikea circularis* sp. nov., holotype female. **1**, ventral view; **2**, genital field; **3**, dorsal view; **4**, palp. (Scale bars: **1**, **3** = 200 µm; **2**, **4** = 50 µm).

relatively short. Lengths of IV-leg-4-6: 112 µm, 138 µm, 130 µm. IV-leg-6 with a row of four pectinate setae and a two normal setae; IV-leg-5 with a row of five pectinate setae. I-leg-5 with two swimming setae, II-leg-5 with two swimming setae, III-leg-3 with one, III-leg-4 with two and III-leg-5 with three swimming setae, IV-leg-3 with one, IV-leg-4 with five and IV-leg-5 with three swimming setae.

Etymology

Named for its rounded body shape.

Remarks

The species is characterised by the very long apodemes of the anterior coxal plates. *Koenikea rotunda* Smit from New Caledonia also has a rounded body shape, but this species has much shorter apodemes, while glandularia 5 of the dorsal shield are located anteriorly of glandularia 3. The male differs from the female in bearing PIV on a short tubercle, but shares the long apodemes and relatively short heavy ventral setae of first and second leg.

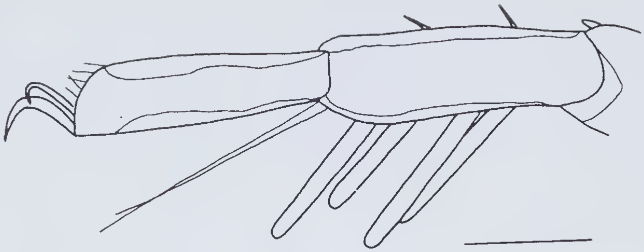
Koenikea (Notomideopsis) crinita Cook

Koenikea crinita Cook, 1986: 197; Harvey, 1998: 142.

Koenikea purpurea Smit, 1992: 105; Harvey, 1998: 142. **New syn.**

Material Examined

Koenikea purpurea Smit



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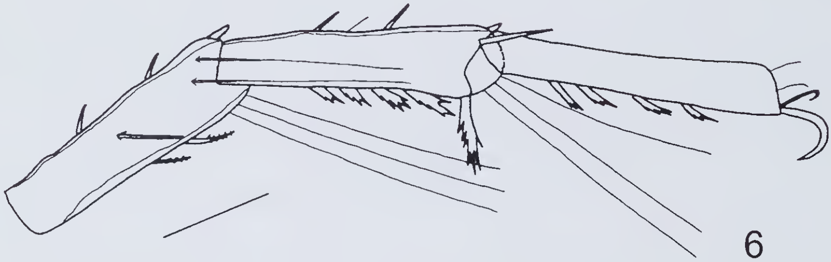

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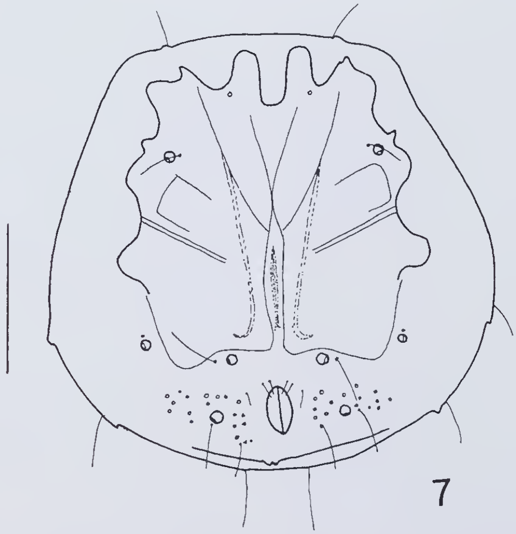

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Figures 5–7 **5**, *Koenikea circularis* sp. nov., holotype female, I-leg-5-6; **6**, *Koenikea circularis* sp. nov., holotype female, IV-leg-4-6. **7**, *Koenikea circularis* sp. nov., paratype male, ventral view. (All scale bars = 50 µm).

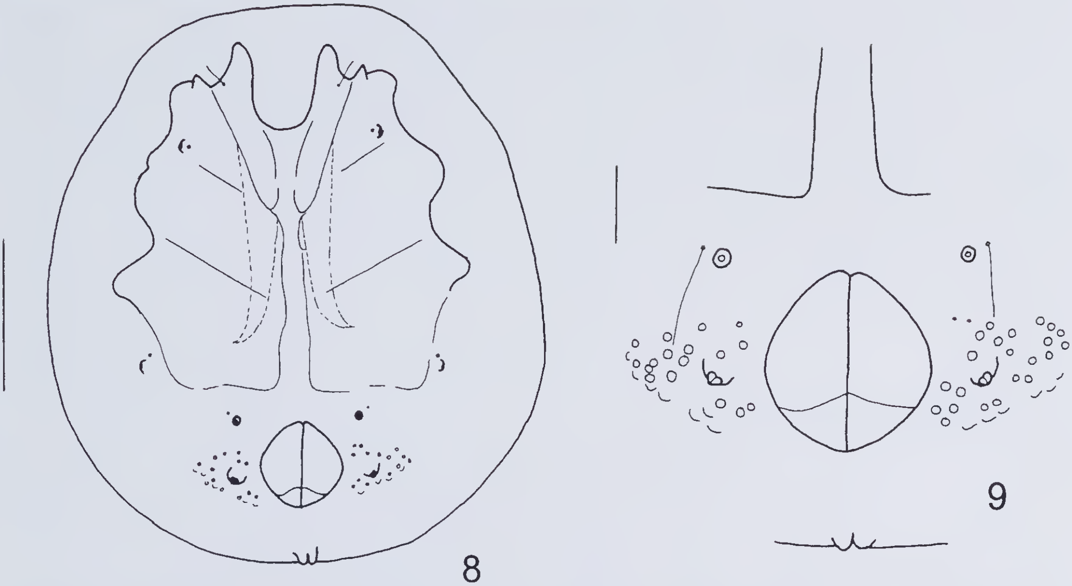
Paratype

Female, Teewah Creek, Cooloola National Park, Queensland, Australia, 22 July 1989 (ZMAN).

Australia: Tasmania: 1 male, 4 females, old river branch Coal River, north of Richmond, 17 October 1997; 2 males, 5 females, Reservoir of Darlington, Maria Island National Park, 18 October 1997; 1 male, Jock's Lagoon, south of St Helens, 20 October 1997. **Victoria:** 1 female, Betka River, at crossing with Stoney Creek Road, southwest of Genoa, 24 October 1997. **New South Wales:** 1 female, School Creek near Morton National Park, 5 November 2001; 1 male, 1 female, Tonoum Brook, Royal National Park, 8 November 2001.

Remarks

My description of *Koenikea purpurea* Smit was based on the conspicuous purple colour and the stiff setae of the coxal plates. However, now that I have seen more specimens of *K. crinita*, it appears that the coxal setae are not as flexible as can be judged from the illustrations of Cook (1986). Therefore, I synonymize *K. purpurea* with *K. crinita*. Colour is apparently a variable character within *K. crinita*. My specimens from Tasmania as well as *K. purpurea* have the glandularia 4 and 5 in a line, while in Cook's illustrated specimens glandularia 4 are located more anteriorly. However, Cook (1986) mentioned variation in the location of glandularia



Figures 8–9 *Koenikea curtiseta* Cook, female; 8, ventral view; 9, detail of genital field. (Scale bars: 8 = 200 µm; 9 = 50 µm).

3, 4 and 5. The females reported by Cook (1986) measured 821–1003 µm in length and 744–927 µm in width. The female reported here from Victoria measured only 599 µm in length and 559 µm in width. The coxal setae of this specimen are finer than those of larger specimens.

Previously, the species has been reported from Tasmania, Victoria, New South Wales and Queensland.

Koenikea (Notomideopsis) curtiseta Cook
Figures 8–9

Koenikea (Notomideopsis) curtiseta Cook, 1986: 188; Harvey, 1998: 142.

Material Examined

Australia: Queensland: 1 male (not completely sclerotized), 1 female, Fitzroy River, Rockhampton, 8 November 1983, leg. A.P. Mackay; 1 female, same location, 6 December 1983; 1 female, Fitzroy River, Yaamba, 20 February 1984, leg. A.P. Mackay; 1 male, Flinders River, 22 June 1983, leg. A.P. Mackay; 4 females, Cockatoo Creek, Cape York Peninsula, 11 September 2000.

Morhpology

Male

Body 664 µm long and 607 µm wide.

Female

Body 713 µm (672–761 µm) long and 632 µm (607–705 µm) wide. Dorsal shield 640 µm long and 567 µm wide. Dorsal shield with six pairs of glandularia, configuration of glandularia as in male. First coxal plates not reaching to anterior body margin. Apodemes of anterior coxal plates reaching beyond suture line of third and fourth coxal plates, occasionally up to middle of fourth coxal plates. Coxoglandularia 2 located halfway between the posterior margin of fourth coxal plates and genital plates. Gonopore 116 µm long. Genital plates with one enlarged glandularium, surrounded by numerous acetabula. Lengths of PI-PV: 24 µm, 78 µm, 42 µm, 70 µm, 28 µm; palp as in male, but setae of dorsal margin of segments heavy. Lengths of I-leg-4-6: 122 µm, 114 µm, 106 µm. Rillborsten of legs I and II short, as in male. Lengths of IV-leg-6: 158 µm, 170 µm, 160 µm. Swimming setae stiff, short and somewhat thickened. Chaetotaxy of swimming setae as in male.

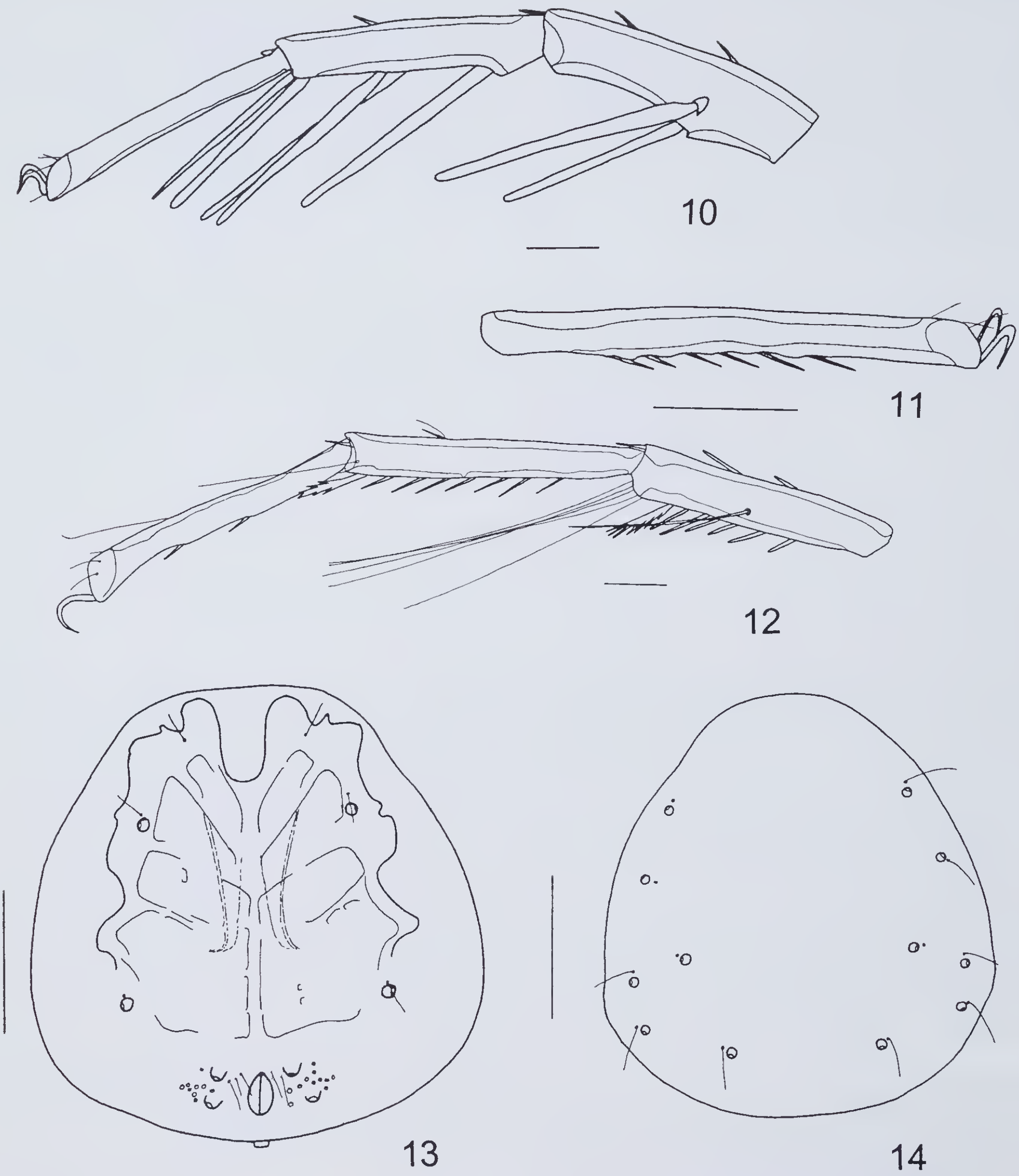
Remarks

The description of Cook (1986) was based on the holotype male only. Therefore, the female is described here for the first time. The species is only known from Queensland.

Koenikea (Notomideopsis) distans K.O. Viets
Figures 10–14

Koenikea distans K.O. Viets, 1980: 160.

Koenikea (Notomideopsis) distans K.O. Viets: Harvey, 1998: 142.



Figures 10–14 10–12 *Koenikea distans* K.O. Viets, holotype female; **10**, I-leg-4-6; **11**, IV-leg-6; **12**, IV-leg-4-6. **13**, **14** *Koenikea distans* K.O. Viets, male; **13**, ventral view; **14**, dorsal view. (Scale bars: **10–12** = 50 µm; **13**, **14** = 200 µm).

Material Examined

Holotype

Female, Morisset Hospital Dam, New South Wales, Australia, 7 September 1977, leg. B.V. Timms (SMF 6724).

Other material

Australia: Queensland: 4 males, Lake Poona via Gympie, 20 July 1980, leg. B.V. Timms (slides SMF 7389, 7390, 7391, 7392); 2 females, Catfish Waterhole, Lakefield National Park, 4 September 2000; 1 female, Hann Crossing (stagnant), Lakefield National Park, 4 September 2000. **New South Wales**: 1 female, Skardon's Lagoon near Cooranbong, 2 January 1977, leg. B.V. Timms (SMF 6450); 1 female, Waterfall Creek at Gunjulla Flat, Royal National Park, 8 November 2001. **Western**

Australia: 2 females, pond Snake Creek, Millstream-Chichester National Park, 17 August 1994; 1 female, pool east side Windjana Gorge, Windjana Gorge National Park, Kimberley, 10 September 1998; 4 females, pool Silent Grove Spring, Kimberley, 11 September 1998 (WAM); 2 males, 5 females, pool Silent Grove (behind ranger station), Kimberley, 11 September 1998 (WAM); 5 males, 19 females, plunge pool, Adcock Gorge, Kimberley, 12 September 1998; 1 female, pool near Adcock Gorge, Kimberley, 12 September 1998; 2 females, pool Galvans Gorge, Kimberley, 12 September 1998; 2 females, Miner's Pool, Drysdale River Homestead, Kimberley, 14 September 1998; 2 males, 1 female, pool Amalia Gorge, El Questro Station, Kimberley, 16 September 1998 (WAM); 1 female, Lake Kununurra, 10 km southeast of Kununurra, 19 September 1998; 2 females, plunge pool Cathedral Gorge, Purnululu National Park, 24 September 1998; 4 females, Palm Springs, south of Halls Creek, 25 September 1998. **Northern Territory**: 2 females, Magela Creek floodplain, Winmurra Billabong, 15 November 1979, leg. R. Tait (slides SMF 7207, 7208); 1 female, pond in Jim Jim Creek, at Jim Jim Crossing, Kakadu National Park, 22 July 1994; 7 males, 2 females, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 1 male, 1 female, Lily Pond Falls, Katherine Gorge National Park, 27 July 1994.

Morphology

Male: Body 640 µm (567–632 µm) long and 640 µm (551–648 µm) wide. Dorsal shield 599 µm long and 551 µm wide. Dorsal shield with six pairs of glandularia, none of which are on tubercles. First coxal plates almost reaching to anterior body margin. Posterior apodemes of anterior coxal plates reaching beyond suture line of third and fourth coxal plates. Genital field located halfway between posterior margin of fourth coxal plates and posterior body margin. Coxoglandularia 2 located close to genital field. Gonopore 72 µm long. Genital field with one large, somewhat bulging glandularium surrounded by approximately 12 small acetabula (but number difficult to ascertain). Lengths of PI-PV: 20 µm, 82 µm, 46 µm, 88 µm, 34 µm; palp as in female. Lengths of I-leg-4-6: 166 µm, 168 µm, 188 µm. Lengths of IV-leg-4-6: 196 µm, 224 µm, 206 µm. Chaetotaxy as in female, but IV-leg-4 with five swimming setae. IV-leg-6 more slender compared to female.

Female: In addition to the original description of Viets (1980) I give here illustrations of the first and fourth leg as well as some measurements. Body 737–879 µm long and 616–786 µm wide. Dorsal shield 656–794 µm long and 571–688 µm wide. Dorsal lengths of I-leg-4-6 of holotype: 200 µm, 186 µm, 180 µm. Dorsal length of IV-leg-4-6 of holotype: 202 µm, 230 µm, 212 µm. Viets (1980) mentioned the presence of a row of eight small setae on IV-leg-4, but actually two rows are present, one of six and one of two setae (compare figures 11 and 12).

Remarks

The original description was based on the holotype female only. The male is therefore described for the first time. Previously, the species was only known from New South Wales, and it is reported here for the first time from Western Australia, the Northern Territory and Queensland. For differences with *K. branacha* and *K. pseudodistans* see under the latter species.

Koenikea (Notomideopsis) gracilipalpis sp. nov.

Figures 15–22

Material Examined

Holotype

Male, plunge pool Edith Falls, Katherine Gorge National Park, Northern Territory, Australia, 30 July 1994 (NTM).

Paratype

Female, Radon Springs, Kakadu National Park, Northern Territory, 19 July 1994 (NTM).

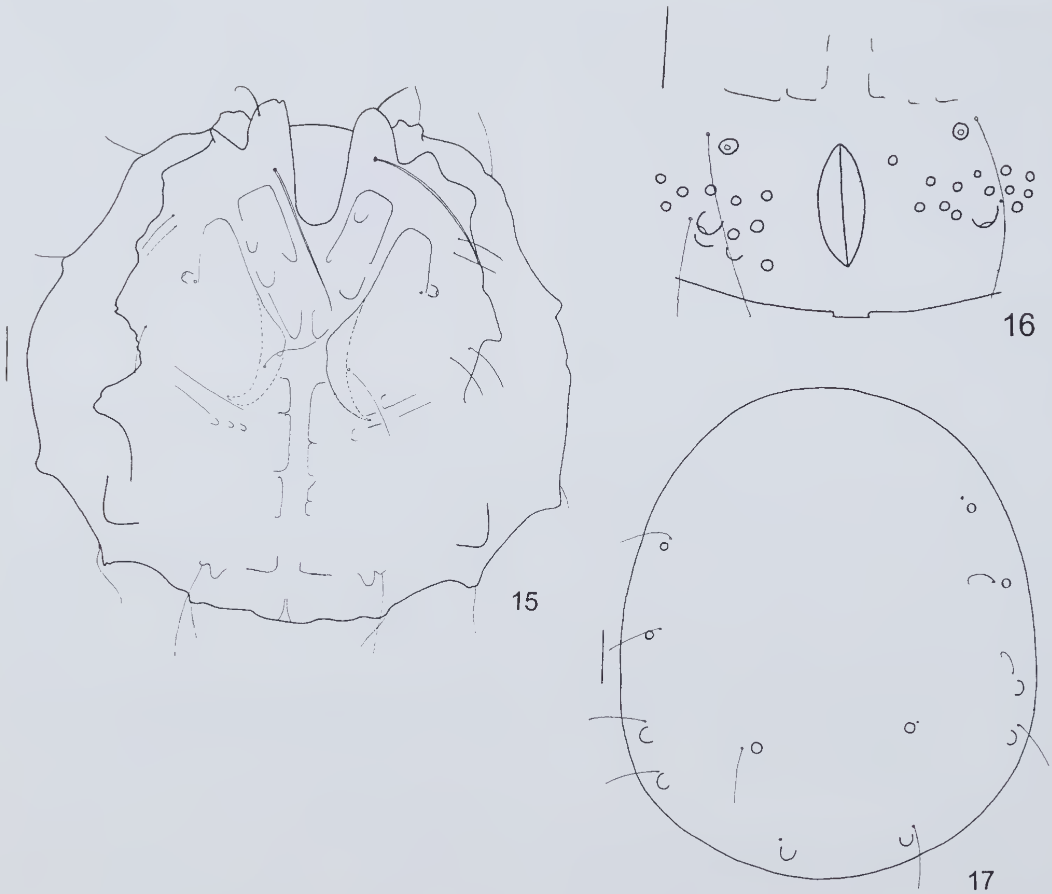
Diagnosis

Very slender palp.

Description

Male

Body 478 µm long and 448 µm wide. Dorsal shield 445 µm long and 393 µm wide. Dorsal shield with six pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. Third, fifth and sixth pair of glandularia on small tubercles. Ventral shield with tubercles near lateral margin. Tips of first coxal plates blunt, extending beyond anterior margin of body; first coxal plates with one pair of long setae. Posterior apodemes of anterior coxal plates extending to suture line of third and fourth coxal plates. Excretory pore terminal. Coxoglandularia 2 located halfway posterior margin of fourth coxal plates and genital field. Gonopore 98 µm long. Genital field with approximately 13 pairs of acetabula. Genital field in normal position, but cannot be seen in Fig. 15 due to skew position in slide. Lengths of PI-PV: 16 µm, 48 µm, 34 µm, 87 µm, 44 µm. Palp slender, especially PV. Lengths of I-leg-4-6: 156 µm, 150 µm, 148 µm. Rillborsten of first and second legs relatively long. Lengths of IV-leg-5-6: 156 µm, 140 µm; IV-leg-6 with two setae on ventral margin. II-leg-5 with one swimming seta, III-leg-4 and 5 with two swimming setae (but number is difficult to



Figures 15–17 *Koenikea gracilipalpis* sp. nov., holotype male; **15**, ventral view; **16**, genital field; **17**, dorsal shield. (All scale bars = 50 µm).

ascertain), IV-leg-4 with two and IV-leg-5 with three swimming setae. Swimming setae relatively short.

Female

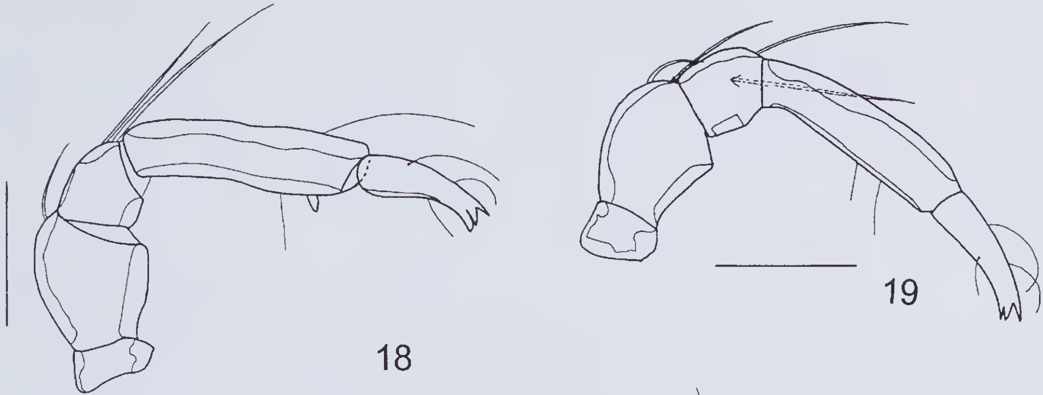
Body 591 µm long and 564 µm wide. Dorsal shield 543 µm long and 494 µm wide. Dorsal shield with six pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. Third, fifth and sixth pair of glandularia on small tubercles. Tips of first coxal plates blunt, extending beyond anterior margin of body; first coxal plates with long setae. Posterior apodemes of anterior coxal plates extending to suture line of third and fourth coxal plates. Gonopore terminal, measurement of length not possible. Excretory pore terminal. Lengths of PI-PV: 18 µm, 54 µm, 38 µm, 90 µm, 50 µm; palp as in male. Lengths of I-leg-4-6: 184 µm, 146 µm, 132 µm. Rillborsten of first and second leg long. Lengths of IV-leg-4-6: 163 µm, 168 µm, 151 µm; IV-leg-6 with 5 setae on ventral margin. I-leg-5, II-leg-4, III-leg-3 and IV-leg-3 with one swimming seta, III-leg-4, III-leg-5 and IV-leg-5 with three swimming setae and IV-leg-4 with five swimming setae. Swimming setae of normal length.

Etymology

Named for its slender palp.

Remarks

The new species shares the long coxal setae with *K. crinita*, but differs in the very slender palp.



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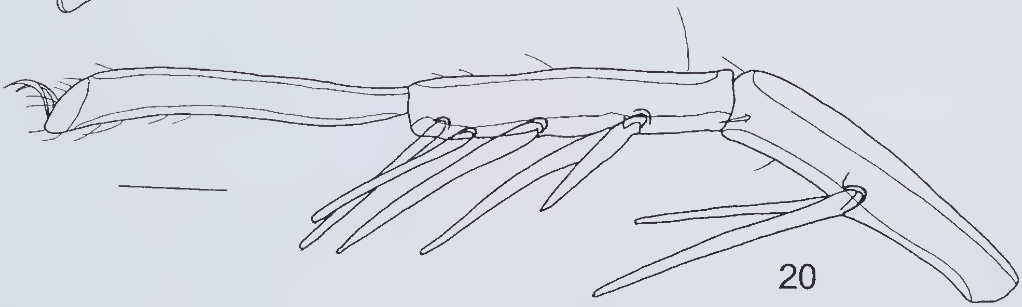

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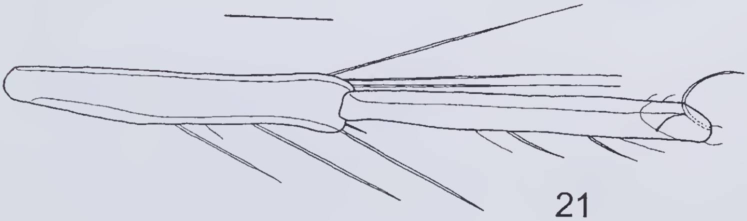

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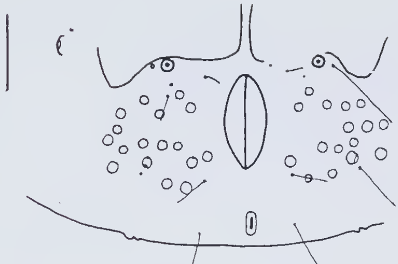
Figures 18–22 **18–21** *Koenikea gracilipalpis* sp. nov., holotype male, **18**, left palp; **19**, right palp; **20**, I-leg-4-6; **21**, IV-leg-5-6; **22**, *Koenikea gracilipalpis* sp. nov., paratype female, genital field. (All scale bars = 50 µm).



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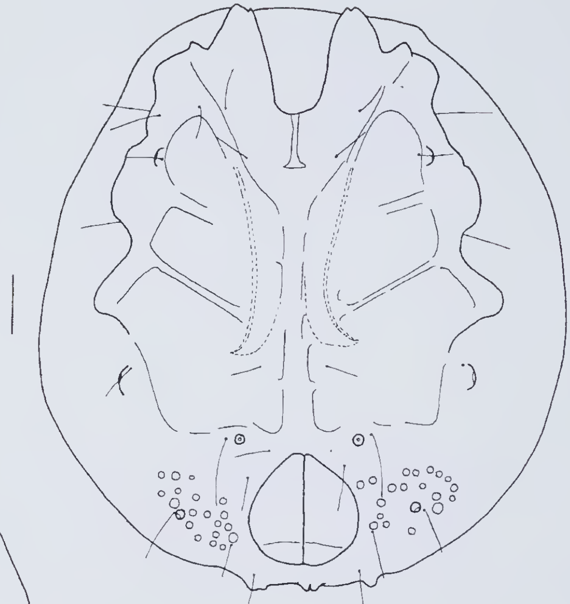

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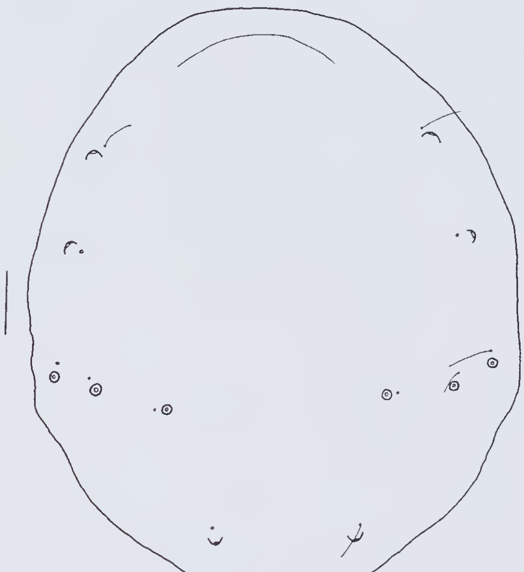

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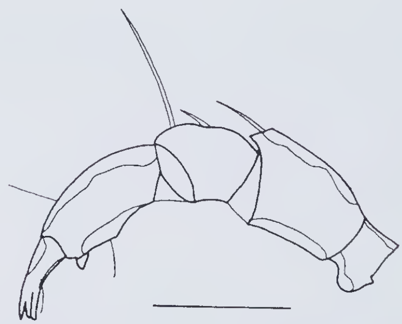

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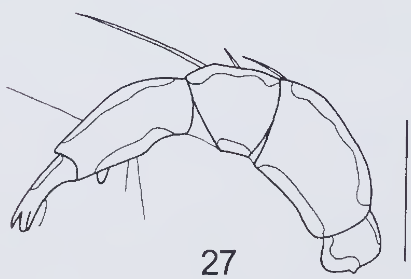

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Figures 23–27 23, *Koenikea* cf *jacunda* Cook, male, detail of genital field; **24**, *Koenikea* cf *jacunda* Cook, female, ventral view; **25**, *Koenikea* cf *jacunda* Cook, female, dorsal shield; **26**, *Koenikea* cf *jacunda* Cook, male, right palp. **27**, *Koenikea* cf *jacunda* Cook, male, left palp (All scale bars = 50 μm).

Koenikea (Notomideopsis) cf. *jacunda* Cook
Figures 23–27

Koenikea (Notomideopsis) jacunda Cook, 1986: 194; Harvey, 1998: 142.

Material Examined

Australia: Northern Territory: 1 male, 2 females, Baboalba Springs (Gubarra), Kakadu National Park, 20 July 1994.

Description

Male

Body 385 µm long and 342 µm wide. Dorsal shield lost during mounting, but glandularia 3, 4 and 5 in a line. First coxal plates extending beyond anterior body margin. Apodemes of first coxal plates extending beyond suture line of third and fourth coxal plates. Coxoglandularia 2 near posterior margin of fourth coxal plates. Gonopore 61 µm long. Genital field with 15–16 acetabula. Glandularium of genital field of same size as surrounding acetabula. Lengths of PI-PV: 17 µm, 42 µm, 34 µm, 52 µm, 32 µm. PIV stocky, tubercle of PIV inserted directly on ventral margin. Lengths of I-leg-4-6: 106 µm, 124 µm, 128 µm. Lengths of IV-leg-4-6: 100 µm, 96 µm, 108 µm. Ventral margin of IV-leg-6 with four setae. Chaetotaxy of swimming setae as described by Cook (1986).

Female

Body 454 µm (478 µm) long and 413 µm (429 µm) wide. Dorsal shield 445 µm long and 365 µm wide. Dorsal shield with six pairs of glandularia. Glandularia 3, 4 and 5 more or less in a line. First coxal plates extending slightly beyond anterior body margin. Coxoglandularia 2 near posterior margin of fourth coxal plates. Gonopore 100 µm long. Genital field with 24–26 acetabula. Glandularium of genital field of same size as surrounding acetabula. Length of PI-PV: 20 µm, 58 µm, 36 µm, 54 µm, 32 µm; palp as in male. Lengths of I-leg-4-6: 110 µm, 104 µm, 108 µm. Lengths of IV-leg-4-6: 110 µm, 132 µm, 130 µm. Chaetotaxy as in male.

Remarks

The male from this study differs from the holotype (the only known specimen known so far) in having a stockier palp, especially PIV. Cook (1986) mentioned that the tubercle of PIV is located on a small tubercle, while it is inserted directly on the segment in my specimen. Moreover, my specimen is smaller, and the leg segments are shorter. However, my specimens have a similar dorsal shield and small size, and are therefore assigned to *K. jacunda,* but this assignment must be considered preliminary.

Koenikea (Notomideopsis) lemba Cook

Koenikea (Notomideopsis) lemba Cook, 1986: 193; Harvey, 1998: 142.

Material Examined

Australia: Victoria: 1 female, Double Creek, Croajingolong National Park, 23 October 1997. **New South Wales**: 14 males, 18 females, Tonoum Brook, Royal National Park, 8 November 2001; 11 males, 27 females, Waterfall Creek at Gunjulla Flat, Royal National Park, 8 November 2001; 1 female, Wattamolla Creek, Royal National Park, 8 November 2001. **Tasmania**: 4 females, Apsley River at crossing with Tasmania Highway, 19 October 1997.

Morphology

Male

Body 737 µm (624–753 µm) long and 632 µm (535–642 µm) wide. Dorsal shield 664 µm long and 559 µm wide. Dorsal shield with six pairs of glandularia, none of which are on tubercles. Glandularia 3, 4 and 5 in a line. First coxal plates not reaching to anterior body margin. Posterior apodemes of anterior coxal plates reaching beyond suture line of third and fourth coxal plates. Coxoglandularia 2 located near posterior margin of fourth coxal plates. Genital plates each with 14 acetabula. Gonopore 92 µm long. Lengths of PI-PV: 24 µm, 88 µm, 40 µm, 90 µm, 40 µm; palp as in female (see Cook, 1986). Lengths of I-leg-4-6: 172 µm, 160 µm, 154 µm. Lengths of IV-leg-4-6: 164 µm, 174 µm, 176 µm. Chaetotaxy of legs as in female. IV-leg-6 with 5-6 setae, the two posterior setae pectinate.

Female

Body 705–895 µm long and 575–786 µm wide. IV-leg-6 with 5-7 setae on ventral margin, the two posterior setae pectinate.

Remarks

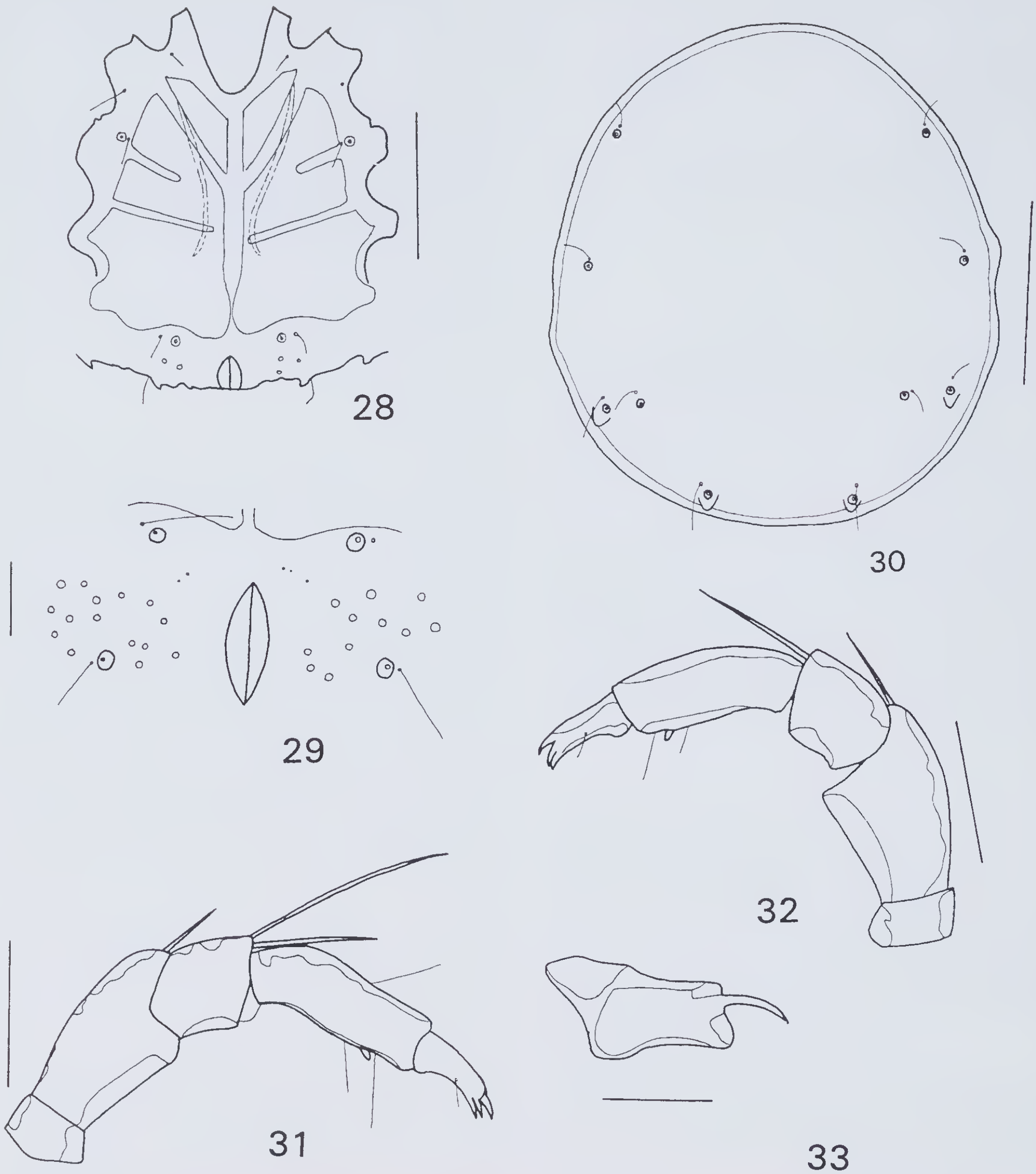
Cook (1986) based his description on three females from Tasmania and New South Wales. Therefore, the male is described here for the first time. As the morphology of the male is similar to that of the female, no illustrations are provided. The species is reported here for the first time from Victoria.

Koenikea (Notomideopsis) lewisensis sp. nov.
Figures 28–38

Material Examined

Holotype

Male, unnamed creek Mt Lewis Road, 900 m a.s.l., Julatten, Queensland, Australia, 14 September 2000 (QM).



Figures 28–33 **28**, *Koenikea lewisensis* sp. nov., holotype male, ventral view; **29**, *Koenikea lewisensis* sp. nov., paratype male, genital field; **30**, *Koenikea lewisensis* sp. nov., holotype male, dorsal shield; **31**, *Koenikea lewisensis* sp. nov., holotype male, palp; **32**, *Koenikea lewisensis* sp. nov., paratype male, palp; **33**, *Koenikea lewisensis* sp. nov., holotype male, chelicere. (Scale bars: **28**, **30** = 200 µm; **29**, **31**, **32** = 50 µm).

Paratypes

Nine males (QM), 8 males (ZMAN), 7 females (QM), 6 females (ZMAN), same data as holotype.

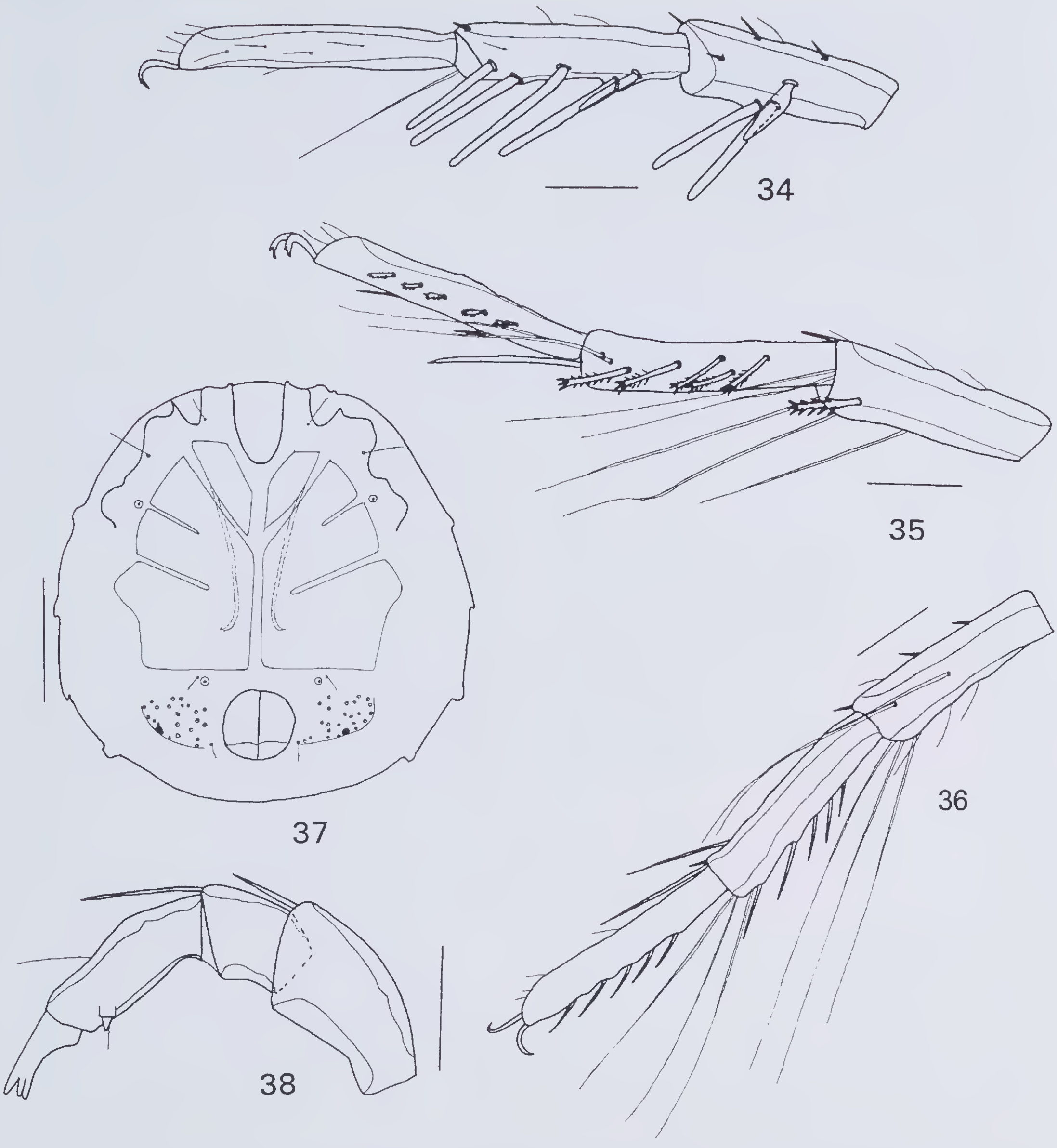
Diagnosis

Dorsal shield with five pairs of glandularia, leg segments short, PIV with a short tubercle.

Description

Male

Body 591 µm (535–575 µm) long and 559 µm (494–550 µm) wide. Body colour orange. Dorsal shield 518 µm long and 478 µm wide. Dorsal shield with five pairs of glandularia on small tubercles; all glandularia near lateral margin of dorsal shield,



Figures 34–38 **34–36** *Koenikea lewisensis* sp. nov., holotype male; **34**, I-leg-4-6; **35**, IV-leg-4-6; **36**, IV-leg-4-6; **37**, *Koenikea lewisensis* sp. nov., paratype female, ventral view; **38**, *Koenikea lewisensis* sp. nov., paratype female, palp (Scale bars: **34–36**, 38 = 50 µm; 37 = 200 µm).

except fourth pair. Ventral shield with tubercles near lateral margin. Tips of first coxal plates blunt, not extending beyond anterior margin of body. Posterior apodemes of anterior coxal plates extending beyond suture line of third and fourth coxal plates. Excretory pore terminal. Genital field of holotype difficult to observe; gonopore of paratype 80 µm long. Genital field of paratypes with 18–19 acetabula on each side. Dorsal lengths of PI-V: 17 µm, 64 µm, 30 µm, 64 µm, 34 µm. Peg-like seta of PIV located on a very short tubercle (better visible in illustrated female). Lengths of I-leg-4-6: 116 µm, 126 µm, 136 µm; I-leg-5 with one long swimming seta. Rillborsten of first and second legs relatively long. Lengths of IV-leg-4-6: 122 µm, 126 µm, 136 µm. IV-leg-5 and -6 with five pectinate setae. IV-leg-5 with three swimming setae, IV-leg-4 with five swimming setae, IV-leg-3 with one swimming seta, III-leg-5 and -4 with three swimming seta, II-leg-5 with two swimming setae and II-leg-4 with one swimming seta.

Female

Body 664 µm (591–721 µm) long and 640 µm (579–680 µm) wide. Dorsal shield 624 µm long and 559 µm wide. Dorsal shield with five pairs of glandularia on small tubercles; all glandularia near lateral margin of dorsal shield, except fourth pair. Tips of first coxal plates blunt, extending to anterior margin of body. Posterior apodemes of anterior coxal plates extending halfway down fourth coxal plates. Gonopore 120 µm long. Genital plates each with 23–24 acetabula. Lengths of PI-PV: 18 µm, 74 µm, 40 µm, 75 µm, 40 µm; palp as in male. Lengths of I-leg-4-6: 140 µm, 134 µm, 136µm. Rillborsten of first and second legs relatively long. Lengths of IV-leg-4-6: 138 µm, 142 µm, 144 µm. Chaetotaxy of legs as in male.

Etymology

Named after Mt Lewis.

Remarks

Only two other Australian *Koenikea* species have the dorsal shield with five pairs of glandularia, i.e. *K. australica* Lundblad and *K. decapora* Cook. The new species differs from both species in much shorter leg segments (e.g. I-leg-6 is 136 µm long in *K. lewisensis* and 214-236 µm and 246 µm respectively in *K. australica* and *K. decapora*). Moreover, the tubercle of PIV is large in *K. australica* and absent in *K. decapora*, while it is short in *K. lewisensis*.

Koenikea (Notomideopsis) pauciacetabulata sp. nov.

Figures 39–45

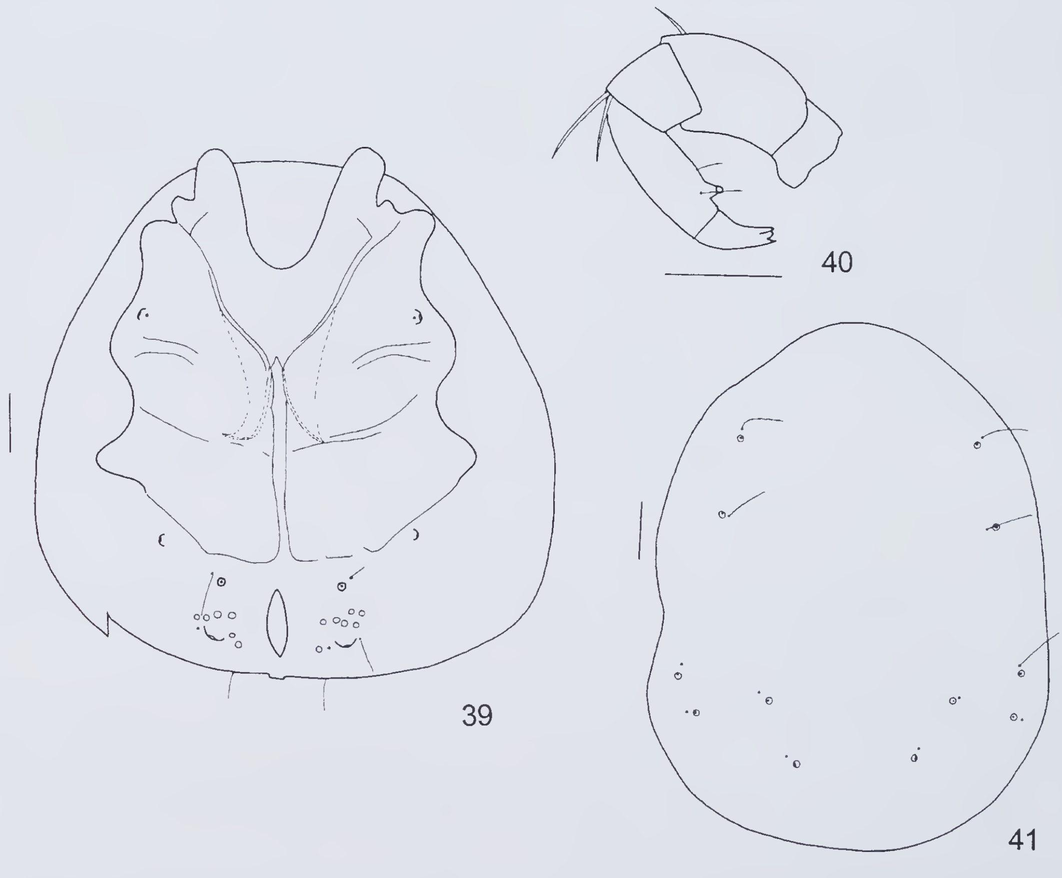
Material Examined

Holotype

Male, Dalhousie Springs, spring Ca1 (pool), South Australia, Australia, 14 June 1985, leg. W. Zeidler & K.L. Gowlett (SAM).

Paratype

Female, same data as holotype (SAM).



Figures 39–41 *Koenikea pauciacetabulata* n. sp., holotype male; **39**, ventral view; **40**, palp; **41**, dorsal shield. (All scale bars = 50 µm).

Other material

Female, not fully sclerotized, same data as holotype (SAM).

Diagnosis

Very few acetabula, male with enlarged claw of IV-leg-6.

Description

Male

Body 445 µm long and 397 µm wide. Dorsal shield 429 µm long and 332 µm wide. Dorsal shield with six pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. Distance between third and fourth pair slightly smaller than distance between fifth and sixth pair. Due to inappropriate fixation in alcohol, not all details visible. First coxal plates extending beyond anterior body margin. Apodemes of anterior coxal plates extending until suture line of third and fourth coxal plates. Coxoglandularia 2 located halfway posterior margin of fourth coxal plates and genital field. Gonopore 58 µm long. Genital plates small, each with 6–7 acetabula, partly surrounding enlarged glandularia. Excretory pore terminal. Lengths of PI-PV: 20 µm, 68 µm, 34 µm, 72 µm, 30 µm. Peg-like seta of PIV on a tubercle, well distanced from distal end of segment. Lengths of I-leg-4-6: 120 µm, 116 µm, 120 µm. First and second legs with long rillborsten. Lengths of IV-leg-4-6: 144 µm, 156 µm, 112 µm. Claw of IV-leg-6 enlarged, 62 µm from base to tip. Ventral margin of IV-leg-6 with a row of 7-8 short setae. III-leg-4 and IV-leg-4 with three swimming setae, III-leg-5 with two and IV-leg-5 with one (two?) swimming setae, but very likely some swimming setae lost. Swimming setae relatively short.

Female

Body 587 µm long and 494 µm wide. Dorsal shield 510 µm long and 397 µm wide. Dorsal shield with six pairs of glandularia. All glandularia near lateral margin of dorsal shield, except fifth pair. First coxal plates not extending beyond anterior body margin. Apodemes of anterior coxal plates extending until suture line of third and fourth coxal plates. Coxoglandularia 2 located halfway between posterior margin of fourth coxal plates and genital field. Gonopore large, 140 µm long. Genital plates small, with 6 pairs of acetabula, partly surrounding enlarged glandularia. Excretory pore terminal. Lengths of PI-PV: 20 µm, 76 µm, 36 µm, 76 µm, 32 µm; palp as in male. Lengths of I-leg-4-6: 138 µm, 120 µm, 116 µm. Rillborsten of first and second legs long. Lengths of IV-leg-4-6: 144 µm, 166 µm, 160 µm. Claw of IV-leg-6 not enlarged, 32 µm in width. Ventral margin of IV-leg-6 with 7-8 setae. III-leg-4 and IV-leg-5 with two swimming setae, III-leg-5 with 3 and IV-leg-4 with five swimming setae.

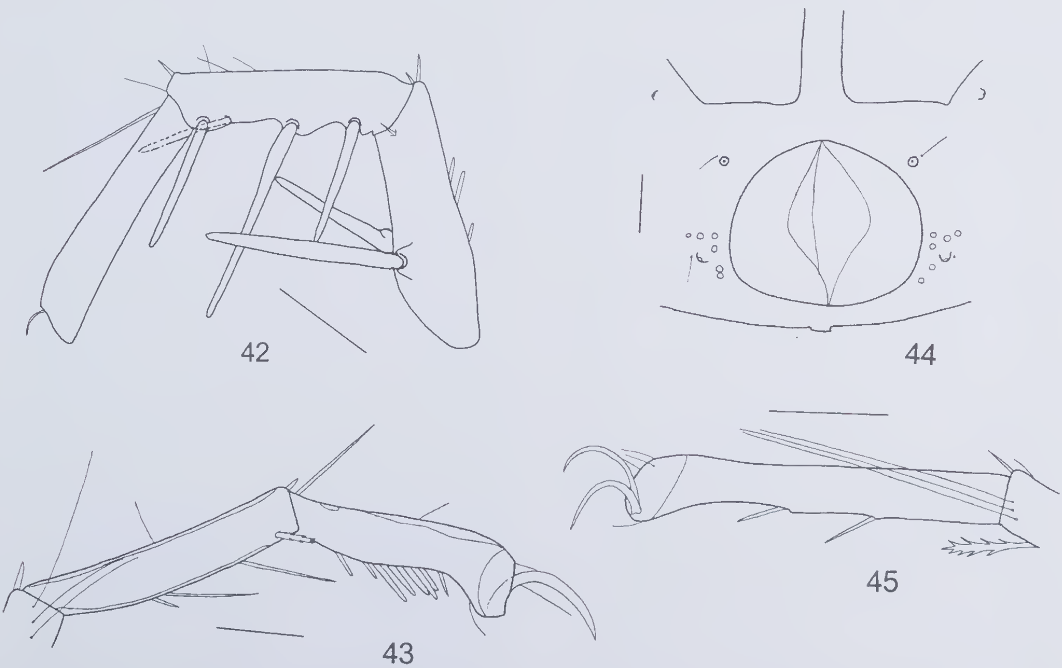


Figure 42–45 **42, 43** *Koenikea pauciacetabulata* n sp., holotype male; **42**, I-leg-4-6; **43**, IV-leg-5-6; **44, 45** *Koenikea pauciacetabulata* n sp., paratype female; **44**, genital field; **45**, IV-leg-6. (All scale bars = 50 µm).

Etymology

Named for its genital field with few acetabula.

Remarks

IV-leg-6 of the male of the new species is very similar to that of *K. pseudodistans*, but it is shorter. Moreover, the male of the new species is smaller, has many fewer acetabula and the coxoglandularia are not located close to the genital field as in *K. pseudodistans*. The configuration of the glandularia on the dorsal shield in the male is somewhat similar to *K. rutala* Cook, but the latter species lacks an enlarged claw. The female has some similarity with *K. rubipes*, which also has genital plates with few acetabula. However, *K. rubipes* has more acetabula (7–10), coxoglandularia 2 are located close to the genital field, and IV-leg-6 is much longer (more than 200 µm).

Koenikea (Notomideopsis) pseudodistans Cook
Figures 46–48

Koenikea (Notomideopsis) pseudodistans Cook, 1986: 192; Harvey, 1998: 142.

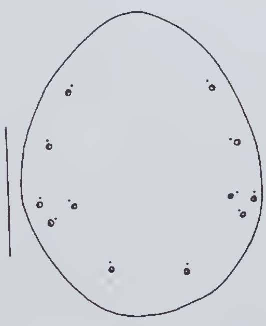
Material Examined

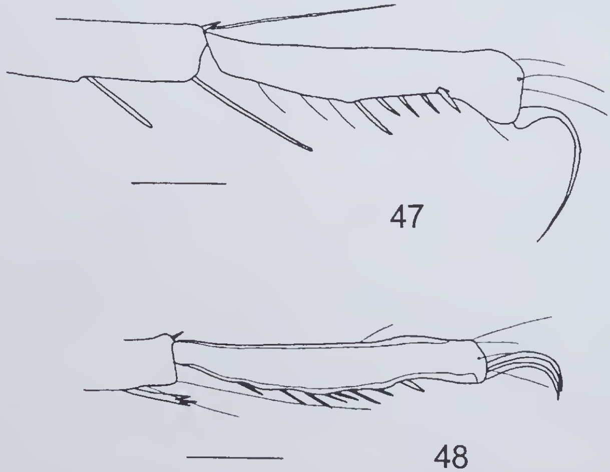
Australia: Western Australia: 1 female, Chinderwariner Pool, Millstream-Chichester National Park, 15 August 1994; 1 male, 1 female, Deep Reach Pool, Millstream-Chichester National Park, 15 August 1994; 1 male, pools upstream of Bell Gorge Falls, Kimberley, 11 September 1998; 1 female, Palm Springs, south of Halls Creek, 25 September 1998. **Northern Territory**: 1 female, Magela Creek floodplain, Winmurra Billabong, 15 November 1979, leg. R. Tait (slide SMF 7206); 1 male, Manton Dam, 1 August 1994. **Queensland**: 1 female, Fitzroy River, Rockhampton, 20 February 1982, leg. A.P. Mackay; 2 males, 2 females, same location, 23 November 1982; 1 male, same location, 4 January 1983; 2 males, 3 females, same location, 11 January 1983; 3 males, 10 females, same location, 1 February 1983; 1 male, 4 females, same location, 1 March 1983; 3 males, 6 females, same location, 15 March 1983; 1 female, same location, 29 March 1983; 3 males, 12 females, same location, 13 April 1983; 1 female, same location, 7 July 1983; 2 males, 2 females, same location, 2 August 1983; 2 males, 22 females, same location, 30 August 1983; 3 females, same location, 27 September 1983; 6 females, same location, 11 October 1983; 3 males, 5 females, same location, 25 October 1983; 17 males, 14 females, same location, 8 November 1983; 1 male, 4 females, 23 November 1983; 10 males, 8 females, same location, 6 December 1983; 1 male, same location, 16 April 1984; 1 female, same location, 3 May 1984; 1 female, same location, 7 June 1984; 1 female, same location, 20 June 1984; 1 male, 1 female, Fitzroy River, Yaamba, 20 February 1981, leg. A.P. Mackay; 1 male, 3 females, same location, 20 February 1984; 1 female, same location, 5 March 1984; 1 female, same location, 2 April 1984; 1 female, same location, 30 May 1984; 1 male, same location, 13 June 1984; 1 female, Nankin Creek, 4 May 1981, leg. A.P. Mackay; 1 male, 2 females, Flinders River, 22 June 1983, leg. A.P. Mackay; 2 females, Lacey Creek, Mission Beach, 17 September 2000.

Description

Male

Body 486–612 µm long and 462–567 µm wide. Dorsal shield 470 µm long and 381 µm wide. Lengths of PI-PV: 18 µm, 67 µm, 45 µm, 76 µm, 31





Figures 46–48 *Koenikea pseudodistans* Cook, male; **46**, dorsal shield; **47**, IV-leg-6; **48**, IV-leg-6. (Scale bars: **46** = 200 µm; **47**, **48** = 50 µm)

µm. Lengths of I-leg-4-6: 160 µm, 154 µm, 176 µm. Lengths of IV-leg-4-6: 172 µm, 200 µm, 152 µm; IV-leg-5 with 8-12 pectinate setae, IV-leg-6 with 8-10 normal setae (but in one of the legs only 6 of these setae are visible). Claws of IV-leg-6 large, 66 µm in width, IV-leg-6 indented distally. II-leg-4, III-leg-3, III-leg-5 and IV-leg-3 with one swimming seta, III-leg-4 with 3, IV-leg-4 with five and IV-leg-5 with two swimming setae. One of the swimming setae of IV-leg-5 reduced in length. Other characters as given by Cook (1986).

Female

Body 745–875 µm long and 662–795 µm wide. IV-leg-6 with 5-10 setae on ventral margin.

Remarks

Males of this species are easily separated from *K. distans* by the enlarged claw of IV-leg-6. However, the separation of the females from *K. distans* with the characters given by Cook (1986) is problematic. Cook (1986) mentioned the following distinguishing characters between the two species: coxoglandularia 2 located more posteriorly in *K. pseudodistans*, gonopore placed well forward in *K. distans* and more near posterior margin in *K. pseudodistans*, the tubercle of the peg-like seta of PIV is more distally located in *K. pseudodistans* and the body of *K. distans* is nearly as wide as long, while it is proportionally narrower in *K. pseudodistans*. Finally, in *K. pseudodistans* the claw of IV-leg-6 of the female is enlarged, but less than in the male. Cook (1986) based his comparison on the holotype of *K. distans* only, as no other specimens were known at that time. Now that I have examined more specimens of *K. distans*, it is clear that the coxoglandularia 2 are also located close to the genital field in *K. distans*. Neither the location of the tubercle of PIV nor the location of the gonopore differ from *K. pseudodistans*. I examined the differences in shape between the females of the two species by using the length/width ratio of the dorsal shield, as this is less deformed in mounted specimens than the body itself. In the two paratype females of *K. pseudodistans*, this ratio is 1.10 and 1.25 respectively, while in the specimens from this study assigned to *K. pseudodistans* the ratio is between 1.17 and 1.23. In females of *K. distans* this ratio varies from 1.12 to 1.16 (1.17) (n=14). In the specimens from the Fitzroy River (Queensland), where only males of *K. pseudodistans* were found, females were found with a ratio up to 1.09. These females had the enlarged claw characteristic for *K. pseudodistans* (see below). Although most females of *K. pseudodistans* are more slender than *K. distans*, this character cannot be used to separate the two species. In my opinion, the only character to separate the females of the two species is the claw of IV-leg-6. The width of this claw, measured from its base to the tip, is 38-42 µm in *K. pseudodistans* and 31–33 µm in *K. distans*. Although females of *K. pseudodistans* usually have a larger IV-leg-6 than *K. branacha*, occasionally an overlap is found. Therefore, the size of the claw is a better character to separate the females of the *K. pseudodistans* and *K. branacha*. The size of the claw of IV-leg-6 of *K. branacha* is 22–30 µm.

Cook (1986) collected the species in Queensland, so it is reported here for the first time from Western Australia and the Northern Territory.

Koenikea (Notomideopsis) rubipes sp. nov.

Figures 49–56

Material Examined

Holotype

Male, Chinderwariner Pool, Millstream-Chichester National Park, Western Australia, Australia, 15 August 1994 (WAM).

Paratypes

1 male, 7 females, same data as holotype (WAM); 1 female, Deep Reach Pool, Millstream-Chichester National Park, Western Australia, 15 August 1994 (ZMAN); 1 female, Crossing Pool, Millstream-Chichester National Park, 16 August 1994 (WAM); 1 male, 8 females, western part Deep Reach Pool, Millstream-Chichester National Park, Western Australia,16 August 1994 (ZMAN).

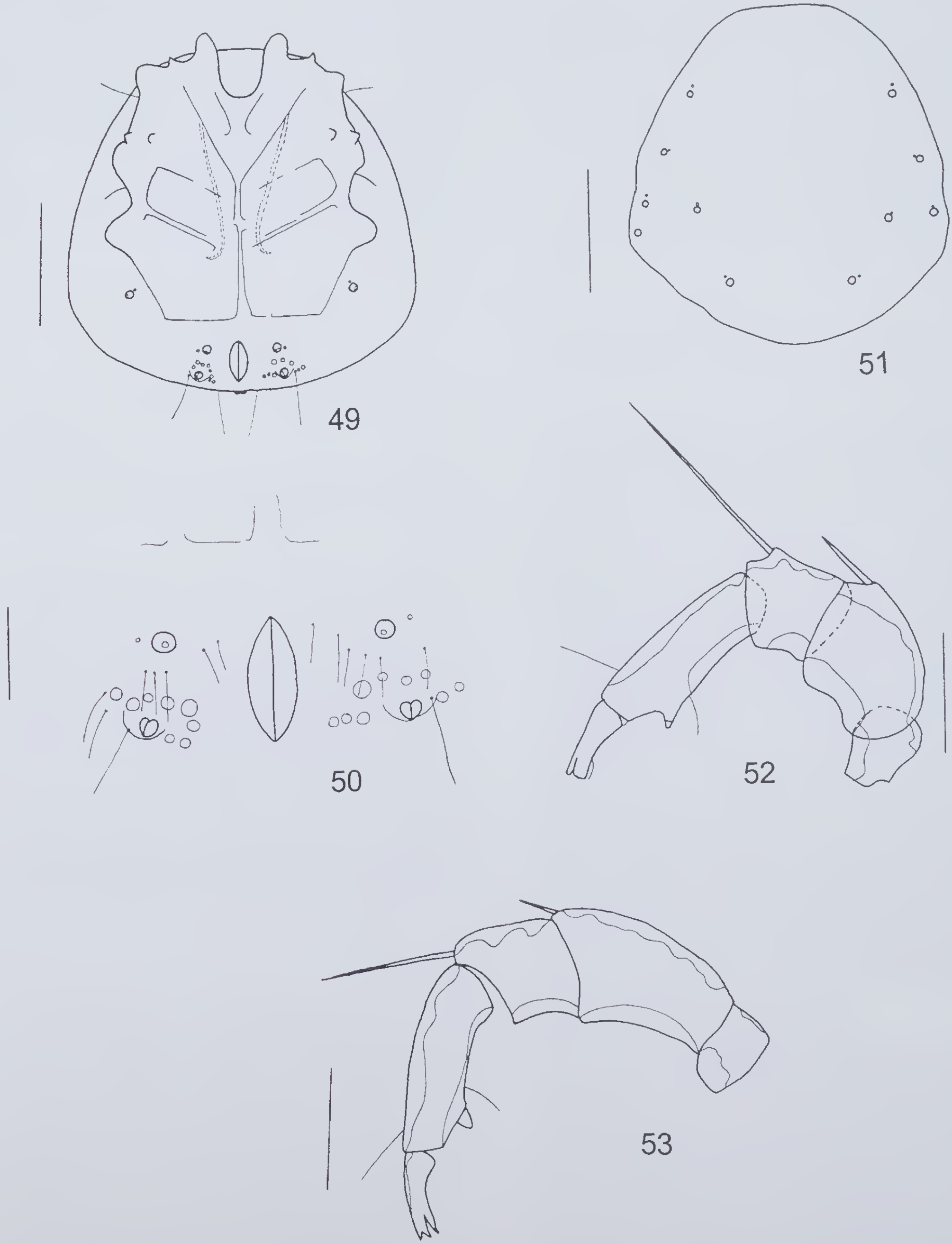
Diagnosis

Genital field small, with only approximately 7–10 acetabula. IV-leg-5 of male with three short swimming setae.

Description

Male

Body 586 µm (543–579 µm) long and 591 µm (522–583 µm) wide. Dorsal shield 559 µm long and 547 µm wide. Dorsal shield with five pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. None of the glandularia on tubercles. Tips of first coxal plates blunt, extending beyond anterior body margin. Posterior apodemes of anterior coxal plates extending beyond suture line of third and fourth coxal plates. Excretory pore terminal. Gonopore 70 µm long. Genital field small, with approximately 7–10 acetabula surrounding an enlarged glandularium. Coxoglandularia 2 lying close to genital field. Lengths of PI-PV: 22 µm, 79 µm, 41 µm, 88 µm, 36 µm. Peg-like seta of PIV on a tubercle, well-distanced from anterior tip of segment. Lengths of I-leg-4-6: 168 µm, 154 µm, 160 µm, these segments with numerous fine setae. Lengths of IV-leg-4-6: 184 µm, 218 µm, 184 µm. IV-

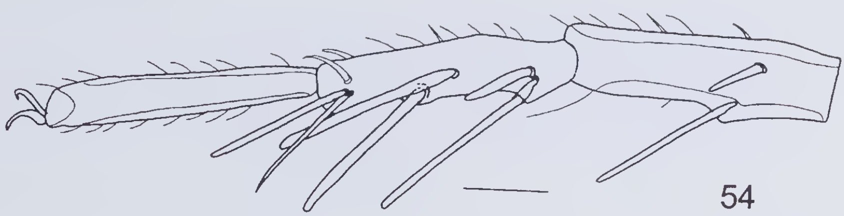


Figures 49–53 *Koenikea rubipes* sp. nov., holotype male, **49**, ventral view; **50**, genital field; **51**, dorsal shield; **52**, left palp; **53**, right palp. (Scale bars: **49**, **51** = 200 µm; **50**, **52**, **53** = 50µm).

leg-6 with 4 (5) small setae, IV-leg-5 with 11 small setae and one large pectinate seta. IV-leg-5 with three short swimming setae, shorter than half of IV-leg-6. Number of swimming setae of other leg segments: IV-leg-3 with one, IV-leg-4 with three, IV-leg-5 with five (not all setae visible in illustrated leg), III-leg-4 and -5 with three swimming setae. All swimming setae stiff, and all legs conspicuously coloured red.

Female

Body 713 µm (624–697 µm) long and 648 µm



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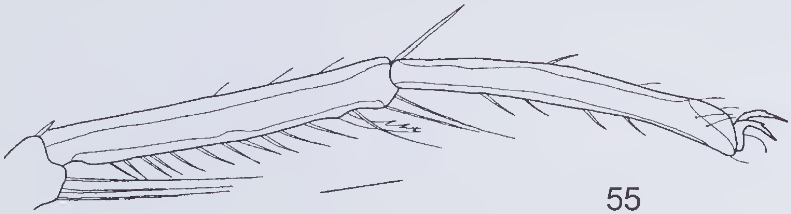

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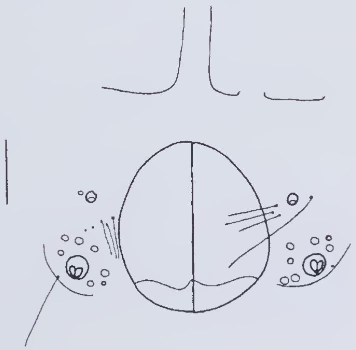

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Figures 54–56 54, 55 *Koenikea rubipes* sp. nov., holotype male; 54, I-leg-4-6; 55, IV-leg-5-6; 56 *Koenikea rubipes* sp. nov., paratype female, genital field. (All scale bars = 50 µm)

(608–632 µm) wide. Dorsal shield 656 µm long and 544 µm wide. Dorsal shield with five pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. None of the glandularia on tubercles. Tips of first coxal plates blunt, extending beyond anterior body margin. Posterior apodemes of anterior coxal plates extending beyond suture line of third and fourth coxal plates. Excretory pore terminal. Gonopore 114 µm long. Genital field small, with approximately 7–10 acetabula surrounding an enlarged glandularium. Coxoglandularia 2 lying close to genital field. Lengths of PI-PV: 30 µm, 98 µm, 52 µm, 96 µm, 42 µm. Lengths of I-leg-4-6: 216 µm, 184 µm, 162 µm. Lengths of IV-leg-4-6: 198 µm, 214 µm, 216 µm. IV-leg-6 with 6-8 small setae, IV-leg-5 with 16 small setae and one large pectinate seta. Chaetotaxy of legs as in male, but swimming setae of IV-leg-5 not shortened.

Etymology

Named for its conspicuous red legs.

Remarks

The new species is close to *Koenikea branacha* and *K. distans*, but differs in the small genital field with few acetabula. Moreover, the swimming setae of IV-leg-5 of the male are much longer in *K. branacha* and *K. distans*.

Koenikea (Notomideopsis) cf. *rutala* Cook

Koenikea (Notomideopsis) rutala Cook, 1986: 189; Harvey, 1998: 142.

Material Examined

Australia: Northern Territory: 1 male, Lily Pond Falls, Katherine Gorge National Park, 27 July 1994.

Remarks

The specimen from this study keys out to *K. rutala*, as the dorsal glandularia 3 and 4 are only slighter closer to each other than 5 and 6. However, my specimen is 470 µm long and 447 µm wide, and therefore smaller than the specimens of Cook (1986), which are 577–582 µm long and 577–608 µm wide. Moreover, the genital field is not terminally placed, and the distance between the genital field and the posterior margin of the fourth coxal plates is larger. The projections associated with the

openings for the fourth legs are somewhat hooked, but beside the configuration of the dorsal glandularia mentioned before, my specimen resembles *K. branacha*, with which it was found. Therefore, its assignment to *K. rutala* is tentative.

Koenikea (Notomideopsis) setosa sp. nov.

Figures 57–63

Material Examined

Holotype

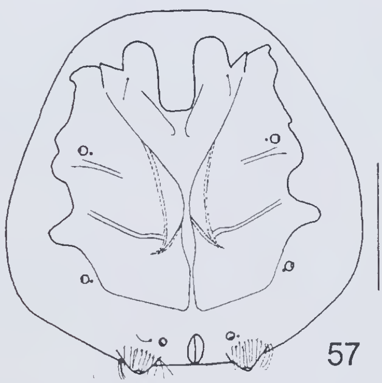
Male, Fortescue River at crossing with North West Coastal Highway, Western Australia, Australia, 18 August 1994 (WAM).

Paratypes

13 males, 4 females, same data as holotype (WAM); 2 males, 4 females, pond Kalamina Gorge (near falls), Hamersley Range National Park, Western Australia, 13 August 1994 (ZMAN); 1 female, Palm Pool, Millstream-Chichester National Park, Western Australia, 15 August 1994 (WAM); 3 males, western part Deep Reach Pool, Millstream-Chichester National Park, Western Australia, 16 August 1994 (ZMAN); 1 female, small pond near Crossing Pool, Millstream-Chichester National Park, Western Australia, 16 August 1994 (WAM); 2 males, Jones River, east of Roeburne, Western Australia, 17 August 1994 (ZMAN); 3 females, pond Snake Creek, Millstream-Chichester National Park, Western Australia, 17 August 1994 (WAM); 1 female, Ashburton River at crossing with North West Coastal Highway, Western Australia, 18 August 1994 (ZMAN); 1 male, Jim Jim Billabong at crossing with Kakadu Highway, Kakadu National Park, Northern Territory, Australia, 22 July 1994 (NTM); 1 male, pool west of Tunnel Creek, Tunnel Creek National Park, Kimberley, Western Australia, Australia, 30 September 1998 (ZMAN).

Other material

Australia: Northern Territory: 1 male, Magela Creek floodplain, Island Billabong, 22 January 1979, leg. R. Tait (SMF 7164).



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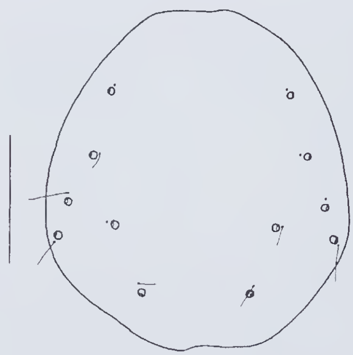

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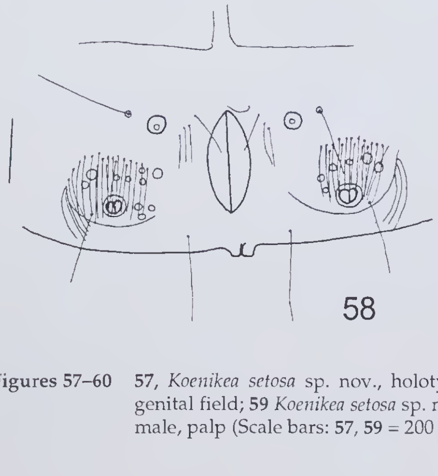

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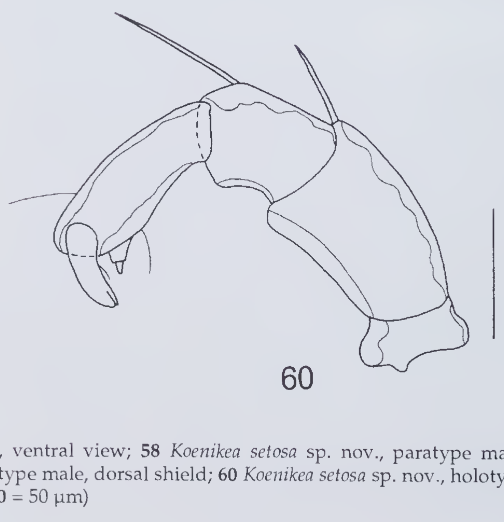

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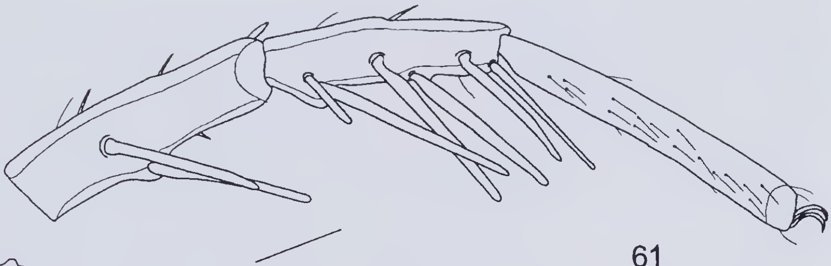
Figures 57–60 **57**, *Koenikea setosa* sp. nov., holotype male, ventral view; **58** *Koenikea setosa* sp. nov., paratype male, genital field; **59** *Koenikea setosa* sp. nov., holotype male, dorsal shield; **60** *Koenikea setosa* sp. nov., holotype male, palp (Scale bars: **57**, **59** = 200 μm; **58**, **60** = 50 μm)



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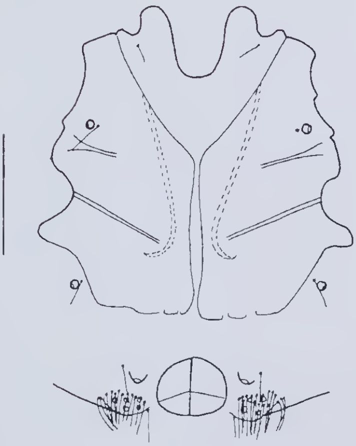

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Figures 61–63 **61, 62** *Koenikea setosa* sp. nov., holotype male; **61**, I-leg-4-6; **62**, IV-leg-5-6; **63** *Koenikea setosa* sp. nov., paratype female, ventral view (Scale bars: **61, 62** = 50 µm; **63** = 200 µm)

Diagnosis

Genital field cone-shaped, with an enlarged, glandularium on top; anterior margin of genital field with numerous small setae.

Description

Male

Body 567 µm (591–640 µm) long and 575 µm (575–640 µm) wide. Dorsal shield 535 µm (543 µm) long and 496 µm (535 µm) wide. Dorsal shield with five pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. None of the glandularia on tubercles. Tips of first coxal plates blunt, not extending beyond anterior margin of body. Posterior apodemes of anterior coxal plates extending beyond suture line of third and fourth coxal plates. Excretory pore terminal. Gonopore 56 µm long. Genital field cone-shaped, with enlarged glandularium on top. Number of acetabula difficult to ascertain, approximately 15–20. Anterior margin of genital field with numerous small setae. Dorsal lengths of PI-V: 18 µm, 80 µm, 56 µm, 84 µm, 35 µm. Peg-like seta of PIV on a distinct tubercle, inserted somewhat distal of anterior tip of segment. Lengths of I-leg-4-6: 158 µm, 140 µm, 176 µm. Rillborsten of first and second legs relatively long. Lengths of IV-leg-4-6: 165 µm, 188 µm, 170 µm. IV-leg-6 with two (four) setae on ventral margin, IV-leg-5 with nine setae and one pectinate seta. The following swimming setae are present: II-leg-4 with one, II-leg-5 with two (but these are very stiff setae), III-leg-4 with three, III-leg-5 with two, IV-leg-3 with one, IV-leg-4 with five and IV-leg-5 with three swimming setae.

Female

Body 794 µm (753–851 µm) long and 688 µm (680–761 µm) wide. Dorsal shield 713 µm long and 591 µm wide. Dorsal shield with five pairs of glandularia; all glandularia near lateral margin of dorsal shield, except fifth pair. Glandularia 3 located somewhat more medially in most females, but in the female from Ashburton River it is distinctly located medially. None of the glandularia on tubercles. Tips of first coxal plates blunt, not extending beyond anterior margin of body. Posterior apodemes of anterior coxal plates extending beyond suture line of third and fourth coxal plates. Excretory pore terminal. Gonopore 104 µm long. Genital field cone-shaped, with enlarged glandularium on top. Number of acetabula difficult to ascertain, approximately 15–20. Lengths of PI-PV: 24 µm, 102 µm, 56 µm, 102 µm, 44 µm; palp as in male. Lengths of I-leg-4-6: 191 µm, 160 µm, 156 µm. Lengths of IV-leg-4-6: 165 µm, 188 µm, 170 µm.

IV-leg-5 with 8-9 of setae (the most distal seta serrated) on ventral margin and one pectinate seta, IV-leg-6 with 4-5 setae on ventral margin. Chaetotaxy of legs as in male.

Etymology

Named for the numerous small setae anterior to the genital field.

Remarks

The configuration of the glandularia of the dorsal shield is similar to that of other Australian species of the genus, but the cone-shaped genital field in combination with the numerous small setae is characteristic for the new species.

Koenikea (Notomideopsis) timmsi K.O. Viets

Figure 64–65

Koenikea (? Koenikea) timmsi K.O. Viets, 1977: 81.

Koenikea (Notomideopsis) timmsi K.O. Viets: Cook, 1986: 190; Wiles, 1997: 410; Harvey, 1998: 142.

Material Examined

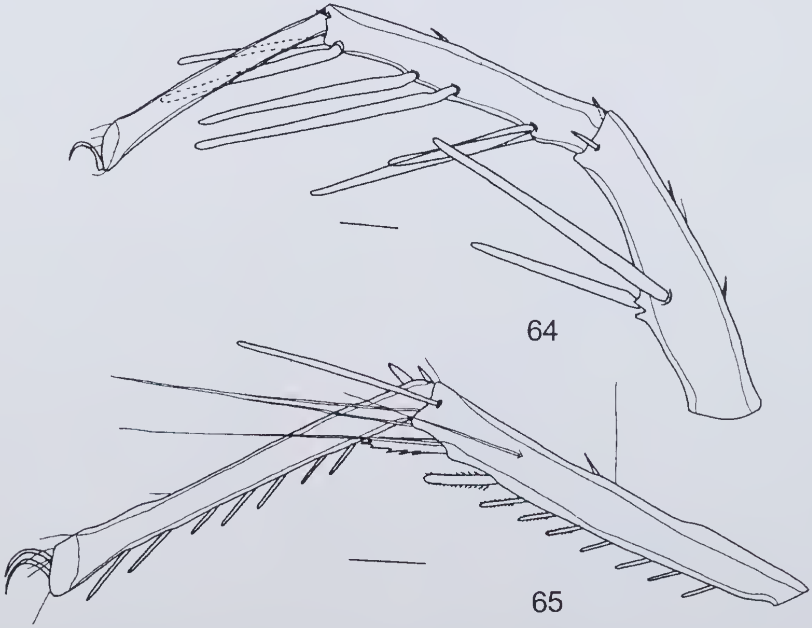
Holotype

Female, Lake Eacham, Queensland, Australia, leg. Timms, 7 July 1974 (SMF 5670).

Other material

Australia: Western Australia: 1 female, pool Lennard River, Windjana Gorge National Park, 9 September 1998; 1 male, 2 females, pool Lennard Gorge, Kimberley, 10 September 1998 (WAM); 4 males, 1 female, pools 3 km from Lennard Gorge, Kimberley, 10 September 1998; 1 female, pools upstream of Bell Gorge Falls, Kimberley, 11 September 1998; 3 males, 6 females, pool Silent Grove (behind ranger station), Kimberley, 11 September 1998 (WAM); 10 males, 4 females, pool Galvans Gorge, Kimberley, 12 September 1998; 1 female, pools downstream of Manning Gorge Falls (at campground), Kimberley, 12 September 1998; 1 male, 4 females, plunge pool Adcock Gorge, Kimberley, 12 September 1998 (WAM); 1 male, pool near Adcock Gorge, Kimberley, 12 September 1998; 2 males, El Questro Gorge, El Questro Station, Kimberley, 15 September 1998; 9 males, 13 females, pool Amalia Gorge, El Questro Station, Kimberley, 16 September 1998; 9 males, 13 females, Middle Springs, west of Kununurra, 18 September 1998 (WAM); 1 male, Spillway Creek, near Lake Argyle, 20 September 1998.

Northern Territory: 1 female, Magela Creek floodplain, Leichhart Billabong, 14 May 1979, leg. Tait (slide SMF 7108); 1 female, Magela Creek floodplain, Driffalo (?) Billabong, 20 July 1979, leg. Tait (slide SMF 7114); 1 male, Radon Springs, Kakadu National Park, 19 July 1994; 1 female, pond Jim Jim Creek, near Jim Jim campground, Kakadu National Park, 23 July 1994; 2 males, 2 females, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 1 male, 1 female, Lily



Figures 64–65 *Koenikea timmsi* K.O. Viets, holotype female; **64**, I-leg-4-6; **65**, IV-leg-5-6. (All scale bars = 50 µm).

Pond Falls, Katherine Gorge National Park, 27 July 1994; 2 females, plunge pool Edith Falls, Katherine Gorge National Park, 30 July 1994.

Morphology

Male

Body 741 µm (575–761 µm) long and 672 µm (538–705 µm) wide; body widened posteriorly. Dorsal shield with six pairs of glandularia, none of which are on tubercles. Five pairs of dorsoglandularia near margin of dorsal shield and one pair situated more medially. First coxal plates extending to anterior body margin. Posterior apodemes of anterior coxal plates reaching beyond suture line of third and fourth coxal plates. In one population (pools 3 km from Lennard Gorge) reaching to the middle of fourth coxal plates. Coxoglandularia 2 a little bit distanced from posterior margin of fourth coxal plates, but closer to posterior margin of fourth coxal plates than to genital plate. Gonopore of paratype 86 µm long. Genital field subterminal, with numerous pairs of acetabula surrounding an enlarged glandularium. Excretory pore terminal. Lengths of PI-PV: 26 µm, 98 µm, 52 µm, 110 µm, 36 µm. Peg-like seta of PIV on a short but distinct tubercle, near distal end of segment. Lengths of I-leg-4-6: 234 µm, 206 µm, 204 µm. Lengths of IV-leg-4-6: 204 µm, 234 µm, 224 µm. IV-leg-6 with nine short setae, IV-leg-5 with one pectinate seta and 11 short setae. The distribution of the swimming setae is as follows: II-leg-4 with 1, III-leg-4 with 2, III-leg-5 with 3, IV-leg-3 with 2, IV-leg-4 with 4 and IV-leg-5 with 3 swimming setae.

Female

Body 810 µm (786–955 µm) long and 721 µm (684–802 µm) wide. Dorsal shield with six pairs of glandularia, none of which are on tubercles. Five pairs of dorsoglandularia near margin of dorsal shield and one pair situated more medially. First coxal plates extending beyond anterior body margin. Coxoglandularia 2 a little bit distanced from posterior margin of fourth coxal plates, but closer to posterior margin than to genital field. Gonopore 146 µm long. Genital field with numerous pairs of acetabula surrounding an enlarged glandularium. Peg-like seta of PIV on a distinct tubercle.

Remarks

Viets (1977) based his description on the holotype female only. In the holotype female the coxoglandularia 2 are located halfway between the posterior margin of the fourth coxal plates and the genital field, but in most specimens I collected they are closer to the posterior margin of the fourth coxal plates. Cook (1986) described the male, but was uncertain of his assignment as his specimen was collected in a stream, while the holotype was collected in a lake. Now that more males have been found, Cook's assignment can be confirmed. In his key, Cook (1986) mentioned that the peg-like seta of PIV is inserted directly on the segment, but from this study it is clear that it is located on a distinct tubercle. The species was previously reported from Queensland, and is reported here for the first time from Western Australia and the Northern Territory.

Koenikea (Notomideopsis) voloma Cook

Koenikea (Notomideopsis) voloma Cook, 1986: 195; Smit, 1992: 104; Harvey, 1998: 142.

Material Examined

Australia: Queensland: 1 female, Broken River near Conical Pool, Eungella National Park, 18 September 2000.

Remarks

Previously known from New South Wales and Queensland.

ACKNOWLEDGEMENTS

I am indebted to Dr Peter Jäger (SMF) for the loan of material from the Viets collection, to Dr Ken Walker and Peter Lillywithe (NMV) for the loan of water mites from the Cook collection and to Dr Davis Hirst (SAM) for sending me material lodged in the South Australiam Museum. Dr Terry Gledhill donated water mites collected by A.P. Mackay in the beginning of the1980s. The national park authorities of Western Australia, the Northern Territory, Queensland, New South Wales, Victoria and Tasmania gave permission to collect in their national parks. Truus van der Pal assisted me with the fieldwork, and Johannes Postma (Ann Arbor) reviewed the English.

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Key to the Australian *Koenikea* species

1. Without apophyses associated with the dorsal shield, apodemes of anterior coxal plates extending to or beyond suture line if third and fourth coxal plates 2

   With apohyses associated with dorsal shield (see Cook, 1986, figure 1047), apodemes of anterior coxal plates extending to middle of third coxal plates .... *Koenikea sorpresa* Cook

2. Five pairs of glandularia on dorsal shield (fig 30) 3

   Six pairs of glandularia on dorsal shield 5

3. I-leg-6 < 150 µm ..... *Koenikea lewisensis* sp. nov.

   I-leg-6 > 200 µm 4

4. Peg-like seta of PIV located on a tubercle (see Cook, 1986, figure 969) .... *Koenikea australica* Lundblad

   Peg-like seta of PIV inserted directly on segment (see Cook, 1986, figure 976) .... *Koenikea decapora* Cook

5. Dorsal shield with one pair of glandularia placed very close together near middle of shield, the other five pairs peripheral (see Cook, 1986, figure 983) ... *Koenikea piota* Cook

   Dorsal shield not with one pair very close together near middle of shield 6

6. Grooved or fluted setae ("rillborsten") of first and second leg relatively short (rillborsten of I-leg-4 shorter than half of segment) (see Cook, 1986, figure 984) .... *Koenikea curtiseta* Cook

   Grooved or fluted setae longer, those of I-leg-4 longer than half of segment (usually nearly as long as segment) 7

7. Glandularia 3, 4 and 5 more or less in a line (see Cook, 1986, figure 1020) 8

   Glandularia 3, 4 and 5 not in a line, but glandularia 3 and 4 much closer to lateral margin than glandularium 4 (figure 17) 10

8. Small species, both male and female < 500 µm, peg-like seta of PIV inserted well before distal end of segment (see Cook, 1986, figure 1021) .... *Koenikea jacunda* Cook

   Larger species, both male and female > 600 µm, peg-like seta of PIV inserted near distal end (see Cook, 1986, figure 1028) 9

9. Peg-like seta of PIV inserted on a long tubercle (peg-like seta shorter than its tubercle), (see Cook, 1986, figure 1018) .... *Koenikea lemba* Cook

   Peg-like seta of PIV inserted on a short tubercle (peg-like seta longer than its tubercle) (seee Cook, 1986, figure 1028) .... *Koenikea voloma* Cook

10. Palp very slender (figure 19) .... *Koenikea gracilipalpis* sp. nov.

    Palp not very slender 11

11. Coxal setae very long, especially of first coxal plates (anterior coxal setae extending beyond suture lines of first and coxal plates) (see Cook, 1986, figures 1039 and 1040) .... *Koenikea crinita* Cook

    Coxal setae not very long 12

12. Glandularia 3 and 4 of dorsal shield only slightly closer to each other on their respective sides than glandularia 5 and 6 are to each other (but when a male, claw of IV-leg-6 not enlarged) (see Cook, 1986, figure 989) .... *Koenikea rutala* Cook

    Glandularia 3 and 4 much closer to each other on their respective sides than 5 and 6 are to each other 13

13. Anterior margin of genital field with numerous small setae (figure 58) .... *Koenikea setosa* sp. nov.

    Anterior margin of genital field with only a few small setae 14

14. Apodemes of first coxal plates very long, reaching to posterior margin of fourth coxal plates (figure 1) .... *Koenikea circularis* sp. nov.

    Apodemes shorter, not reaching posterior margin of fourth coxal plates 15

15. Very slender species, length/width ratio of dorsal shield 1.47 (see Cook, 1986, figure 1030) .... *Koenikea rodosa* Cook

Not as slender, length/width ratio of dorsal shield less than 1.25 16

16. Genital field small, with fewer than 10 acetabula 17

Genital field larger, with more than 10 acetabula 18

17. Coxoglandularia 2 halfway between posterior margin and genital field, genital plates with 6–7 acetabula (figure 44), IV-leg-6 < 180, IV-leg-6 of male enlarged .... *Koenikea pauciacetabulata* sp. nov.

Coxoglandularia 2 close to gential field, genital plates with 7–10 acetabula (figure 56), IV-leg-6 > 200, IV-leg-6 of male not enlarged .... *Koenikea rubipes* sp. nov.

18. Coxoglandularia 2 located near posterior margin of fourth coxal plates (see Cook, 1986, figure 996), tubercle of PIV near distal end (see Cook, 1986, figure 994) .... *Koenikea timmsi* K.O. Viets

Coxoglandularia 2 located closer to genital field, tubercle of PIV located well anterior to distal end of segment 19

19. Claw of IV-leg-6 large (figure 47), in male 60–70 µm in width (= from tip of claw to base), in female 38–42 µm in width .... *Koenikea pseudodistans* Cook

Claw of IV-leg-6 smaller 20

20. IV-leg-6 in male < 180 µm, < 170 µm in female, small species .... *Koenikea branacha* Cook

IV-leg-6 in male > 190 µm, in female > 200 µm, large species .... *Koenikea distans* K.O. Viets

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The genus *Metacyclops* Kiefer in Australia (Crustacea: Copepoda: Cyclopoida), with description of two new species

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Abstract – Two new species of the genus *Metacyclops* Kiefer, 1927 are described from subterranean waters of Western Australia, one from the Kimberley region and the other from the Pilbara region. They both belong to the "*trispinosus*"-group, which has a clear Eastern Gondwana connection and the centre of diversity in Australia. A phyletic tree of this group in Australia is proposed. *Metacyclops kimberleyi* sp. nov. is distinguished from other members of the group by at least two autapomorphies: the exceptionally long dorsal seta on the caudal rami and the maxilliped with only seven armature elements. The only clear autapomorphy of *M. pilbaricus* sp. nov. seems to be its unusual body shape. An antenna without exopod and the second endopodal segment of this appendage with only six setae is a synapomorphy that suggests a close relationship between these two new species. As the genus *Metacyclops* in Australia already has seven valid species, a key to aid in their identification, as well as a map of their distributions, are presented.

INTRODUCTION

At the beginning of the last century the famous Norwegian carcinologist G. O. Sars described *Cyclops arnaudi* based upon material collected by O. A. Sayce in 1901 from a swamp at St. Arnaud in Victoria (Sars, 1908). This species later became the first Australian representative of the genus *Metacyclops*, which was initially established as a subgenus of the genus *Mesocyclops* Sars, 1914 by Kiefer (1927). More than half a century after *Metacyclops arnaudi* was first described, intense investigation of the limnological characteristics of many Australian inland surface waters yielded numerous invertebrate specimens (Bayly, 1964; Bayly and Williams, 1964; 1966a; 1966b). Cyclopoid copepods from those studies were sent for identification to F. Kiefer in Germany, who reported *M. arnaudi* for the second time from two lakes in Victoria (Kiefer, 1967) and also described a new subspecies of this species from a lake in South Australia. However, recent reexamination of that material by Fiers (2001) showed that Kiefer (1967) was not dealing with *M. arnaudi* at all and, furthermore, transferred both taxa into the newly described genus *Meridiecyclops*. Unfortunately, the type material of *M. arnaudi* is no longer available (Hamond, 1987), so the original description of Sars (1908), with its fine illustrations, is all that was left of the first Australian *Metacyclops*. An unnamed and as yet undescribed species of *Metacyclops* was reported by Timms and Morton (1988), but this genus does not appear to have a significant diversity in Australian surface waters, and certainly nothing that could be compared with other continents of the Southern Hemisphere (see Dussart and Defaye, 1985).

Australian subterranean waters, on the other hand, were not investigated systematically until the last decade (Humphreys, 2001). Unexpectedly, the groundwater calcrete aquifers in the Australian arid zone come to the attention of stygobiologists and systematists on account of the diverse obligate stygofauna that is being found there by W. F. Humphreys and his colleagues from the Western Australian Museum (Humphreys, 1993). An unfolding plethora of stygal biodiversity has been found, including a number of higher order taxa variously new to science (e.g. Wilson and Ponder, 1992; Poore and Humphreys, 1992; 1998; Yager and Humphreys, 1996; Danielopol *et al.*, 2000; Jaume and Humphreys, 2001; Jaume *et al.*, 2001). The freshwater cyclopoids collected during that period were sent for identification to G. L. Pesce and his colleagues in Italy, who described *Metacyclops mortoni* from Cape Range peninsula and the Ashburton River, as the first subterranean representative of this genus in Australia (Pesce *et al.*, 1996). This species was later found at two additional localities in the Pilbara Region (Port Hedland and Cossack near Karratha) by De Laurentiis *et al.* (1999). Two years later, the same authors (De Laurentiis *et al.*, 2001) assigned two other cyclopoid species from Western Australia to the genus *Metacyclops*. The first one, *M. fiersi*, was described as a new species from three bores near Eneabba, while the second one was reported as *M.*

cf. monacanthus Kiefer, 1928 from a number of bores at Paroo Station in the Murchison Region. In my recent study of the subterranean copepods from the Murchison Region (Karanovic, 2004) *M. fiersi* was found at 24 additional localities, but it was also transferred into the newly described genus *Fierscyclops*. De Laurentiis *et al.* (2001) noticed some differences between their material and the original description of *M. monacanthus* (Kiefer, 1928), which was known only from New Zealand (Kiefer, 1928), but they made a compromise and assigned it provisionally as *con forme*. I studied that species from 44 different localities from the Murchison Region and have found a number of differences between it and the New Zealand representative (although the type material was not examined), so it was described as a new species (*M. laurentiisae*) in Karanovic (2004). In the same monograph two other new species of the genus *Metacyclops* were described (*M. superincidentis* and *M. pilanus*) and one new group of species, with the clear Eastern Gondwana connection, was established. In this paper two new species from the same group are described, one from the Kimberley, the other one from the Pilbara regions of Western Australia.

Together with the two new species, the genus *Metacyclops* has now seven representatives in Australia. At the end of this paper a key to aid in their identification and a map of their distributions are presented.

MATERIAL AND METHODS

Samples were collected with haul-nets (mesh size 250 or 350 micrometers) from groundwater monitoring bores that are made by mining companies for the purpose of water monitoring. Sometimes they are originally made for water abstraction or mineral exploration and later converted into monitoring bores. They are usually 10 to 20 cm in diameter, and may be lined entirely, or in part, by PVC tubing (the casing). This tubing may be open only at the bottom, or it may be pierced at one or more levels by holes of various sizes, referred to as "slots". The top may be securely capped or entirely open to the elements. Haul-nets are actually simple plankton nets of a different size suitable for the bore, which can range from 30 to 180 mm in diameter. Weighed nets were lowered down into the bore with one bottle screwed on its distal part than hauled through the water column, usually a number of times. All samples were sorted while alive under a dissecting microscope and the copepods were then fixed in 70% ethanol and assigned a field number (prefix BES). Many bores established for hydrogeological work, mineral exploration and water monitoring have prefixes or suffixes of relevance only to that drilling program. These codes are cited in the examined material for both species to aid specification of the location.

Specimens were dissected in Faure's medium, which was prepared following the procedure discussed by Stock and Vaupel Klein (1996). Dissected appendages were covered with a coverslip. For the urosome or the whole animal two human hairs were mounted between the slide and coverslip, so the parts could not be squashed. By moving the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination water slowly evaporated, and appendages or whole animals eventually remained in completely dry Faure's medium. All drawings were prepared using a drawing attachment (tube) on a Leica-DMLS brightfield compound microscope, with C-PLAN achromatic objectives. Specimens that were not drawn were examined in a mixture of equal parts of distilled water and glycerol and, after examination, were again preserved in 70% ethanol. Samples for the scanning electron microscopy were couted in gold and observed under the LEO FEG VPSEM microscope on the in-lens detectors, with working distances between 2 and 6 mm and accelerating voltages between 2 and 5 kV. All the material is deposited in the Western Australian Museum, Perth (prefix WAM).

Morphological terminology follows Huys and Boxshall (1991), except for the swimming legs armature formula, where a much more simplified version is used.

SYSTEMATICS

Family Cyclopidae Burmeister, 1834

Subfamily Cyclopinae Dana, 1853

Genus *Metacyclops* Kiefer, 1927

Metacyclops kimberleyi sp. nov.

Figures 1, 2, 4–28, 46, 48 and 50

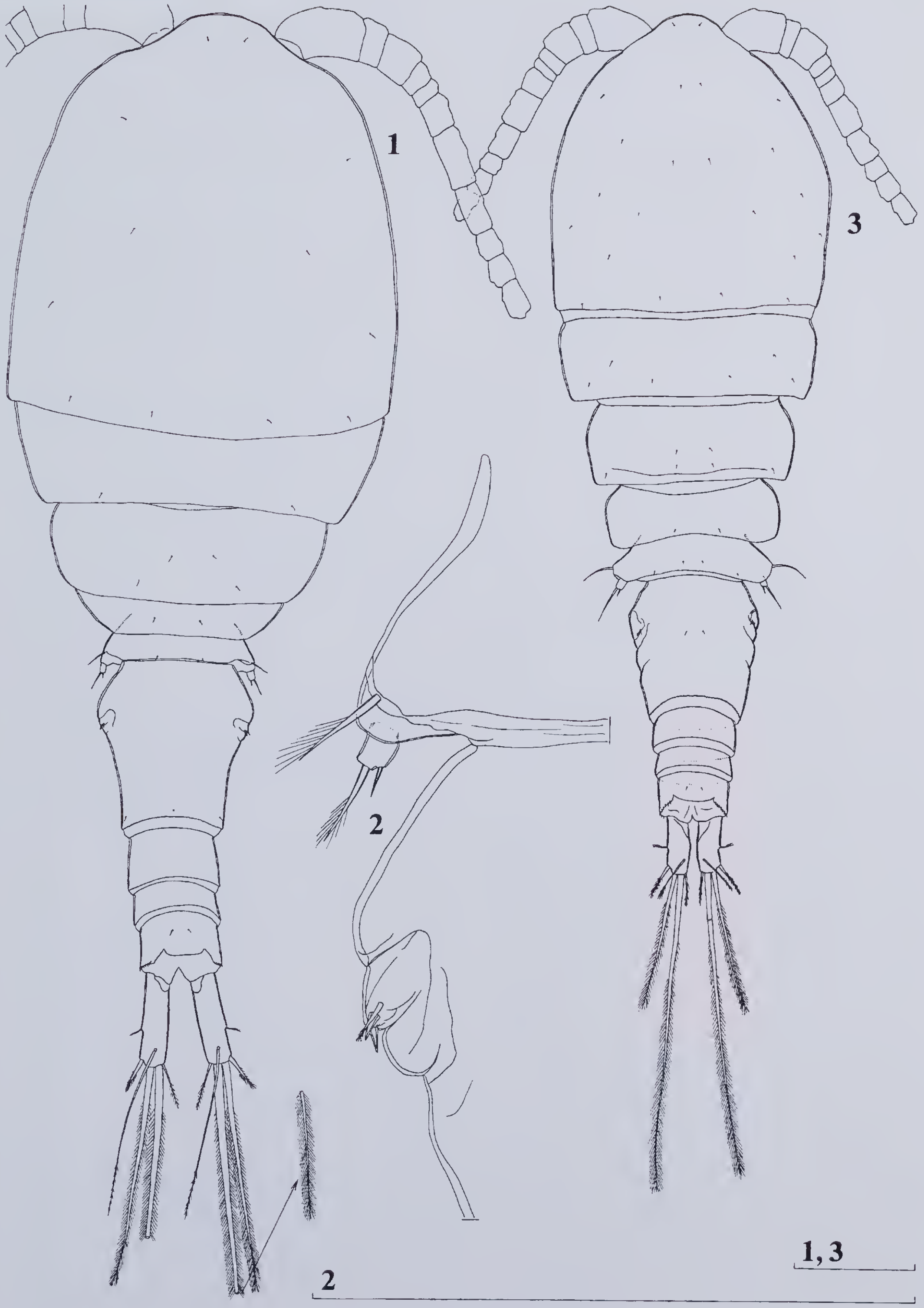
Material Examined

Holotype

Female (WAM C28628), Western Australia, Kimberley, Argyle Diamond Mine, groundwater monitoring bore 29D, 16°41'37"S, 128°27'11"E, 10 October 2002, leg. W. F. Humphreys and R. Webb (BES 9693): dissected on two slides.

Allotype

Male (WAM C28629), Western Australia, Kimberley, Argyle Diamond Mine, groundwater monitoring bore 29D, 16°41'37"S, 128°27'11"E, 10 October 2002, leg. W. F. Humphreys and R. Webb (BES 9693): dissected on two slides.



Figures 1–3 *Metacyclops kimberleyi* sp. nov., holotype (female): 1 – habitus, dorsal view; 2 – left fifth and sixth legs, dorsal view; *Metacyclops pilbaricus* sp. nov., holotype (female): 3 – habitus, dorsal view. Scales = 0.1 mm.

Figures 4–8 *Metacyclops kimberleyi* sp. nov., holotype (female): 4 – urosome, ventral view; 5 – antenna; 6 – maxillula, arthrite of praecoxa; 7 – mandibular palp; 8 – maxilla. Scales = 0.1 mm.

Paratypes

Western Australia, Kimberley, Argyle Diamond Mine, groundwater monitoring bore 29D, 16°41'37"S, 128°27'11"E, 10 October 2002, leg. W. F. Humphreys and R. Webb (BES 9693): one female on SEM stub, couted in gold (WAM C28630) + four copepodids in alcohol (WAM C28631).

Other material

Western Australia, Kimberley, Argyle Diamond Mine, groundwater monitoring bore 30S, 16°41'22"S, 128°27'05"E, 10 October 2002, leg. W. F. Humphreys and R. Webb (BES 9699): three copepodids in alcohol (WAM C28632).

Description

Female (holotype). Body length, excluding caudal setae, 0.862 mm. Habitus (Figure 1) robust, with prosome/urosome ratio 1.4 and greatest width at posterior part of cephalothorax. Body length/width ratio about 2.8; cephalothorax almost 2.5 times as wide as genital double-somite. Rostral expansion well developed. Free pedigerous somites without particular expansions laterally. Colour of preserved specimen yellowish. Nauplius eye not visible. Rostrum well developed, membranous, broadly rounded and furnished with two large sensillae. Cephalothorax somewhat longer than wide; represents 40% of total body length. Surface of cephalothorax shield with few large sensillae, smooth (without minute cuticular pits). Whole body very smooth, with only a few sensillae on prosomites. Hyaline fringes of prosomites narrow and smooth. Fifth pedigerous somite ornamented with 2 dorsal large sensillae and 2 lateral ones; hyaline fringe smooth both dorsally and ventrally (Figures 2, 4 and 11). Genital double-somite slightly longer than wide (ventral view), ornamented with 2 large lateral sensillae; hyaline fringe finely serrated both ventrally and dorsally. Copulatory pore very small, rounded, situated at distal end of first third of somite length; copulatory duct narrow, sclerotized and siphon-shaped. Seminal receptacle relatively large, represents 45% of double-somite's length, with clearly divided anterior and posterior expansions; anterior expansion about 1.2 times as long as posterior one (Figures 4 and 11). Ovipores situated dorsolaterally, covered with reduced sixth legs. Third and fourth urosomal somites unornamented, with irregularly serrated fringes both ventrally and dorsally; third somite about 1.6 times as long as fourth somite. Anal somite with smooth, straight, anal operculum, which somewhat produced posteriorly, but not reaching posterior margin of somite; ornamented with 2 large sensillae dorsally and transverse row of spinules on posterior margin (Figures 9 and 15). Anal sinus smooth.

Caudal rami (Figures 4, 9 and 15) slightly divergent, with space between them of about 0.6 of 1 ramus width, and 3.4 times as long as wide; ornamented with few spinules at base of lateral and outermost apical setae, smooth. Dorsal seta very long, about 2.1 times as long as ramus, inserted at 5/6 of ramus length, uniarticulate at base and bipinnate at distal part. Lateral seta arising at 3/5 of ramus length, shorter than ramus width. Outermost apical seta very stout, spiniform, about 0.46 times as long as ramus, bipinnate. Innermost apical seta about 0.26 times as long as dorsal one, and almost 1.2 times as long as outermost apical seta. Principal apical setae without visible braking planes; inner seta about 1.5 times as long as outer one, and 0.34 times as long as body length.

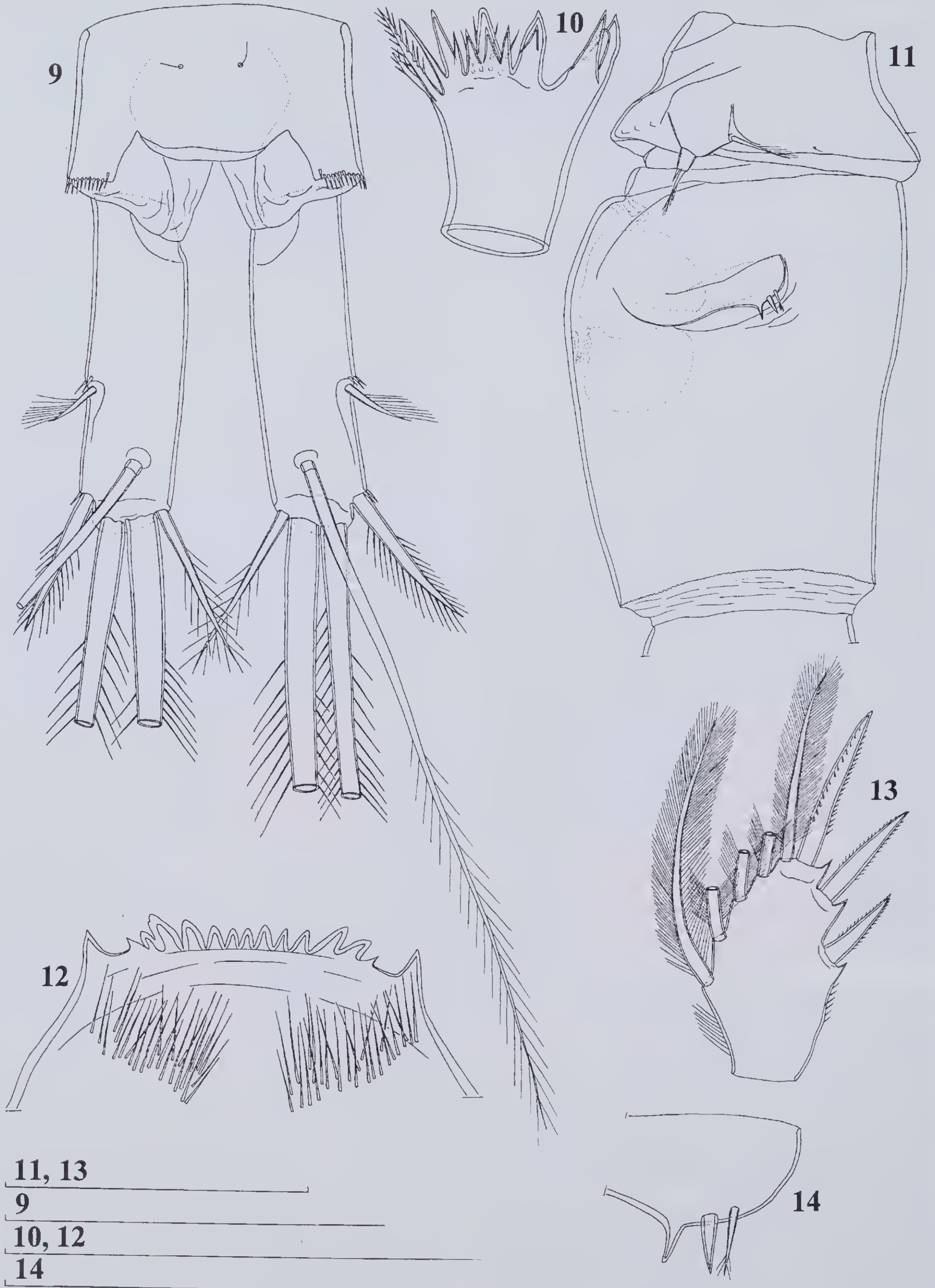
Antennula (Figure 16) 11-segmented, almost reaching posterior margin of cephalothorax, with slender aesthetascs on eighth and eleventh segments and setal formula as follows: 7.4.6.2.2.2.3.2.2.3.7. Just one seta on fourth segment articulating on basal part. One seta on fifth segment spiniform and very short. Just 12 setae (30%) pinnate at distal part (mostly longer and stronger setae); other setae smooth. First segment ornamented with arched row of spinules on anterior surface; other segments with no ornamentation visible. Length ratio of antennular segments, from proximal end and along caudal margins, 1 : 0.3 : 0.5 : 0.2 : 0.15 : 0.4 : 0.9 : 0.7 : 0.3 : 0.4 : 0.5.

Antenna (Figure 5) 4-segmented, comprising relatively large coxobasis and 3-segmented endopod; ornamented with longitudinal rows of minute spinules along posterior margin of endopodal segments. Coxobasis about 2.3 times as long as wide, ornamented with three small groups of minute spinules, armed with 2 smooth setae at distal inner corner; seta representing exopod absent. First endopodal segment armed with 1 smooth seta. Second endopodal segment about twice as long as wide, armed with 6 setae (4 lateral, 1 subapical, and 1 apical). Third endopodal segment about 3 times as long as wide, armed with 7 apical setae. All setae smooth, except longest apical one, which ornamented with short row of minute spinules at midlength.

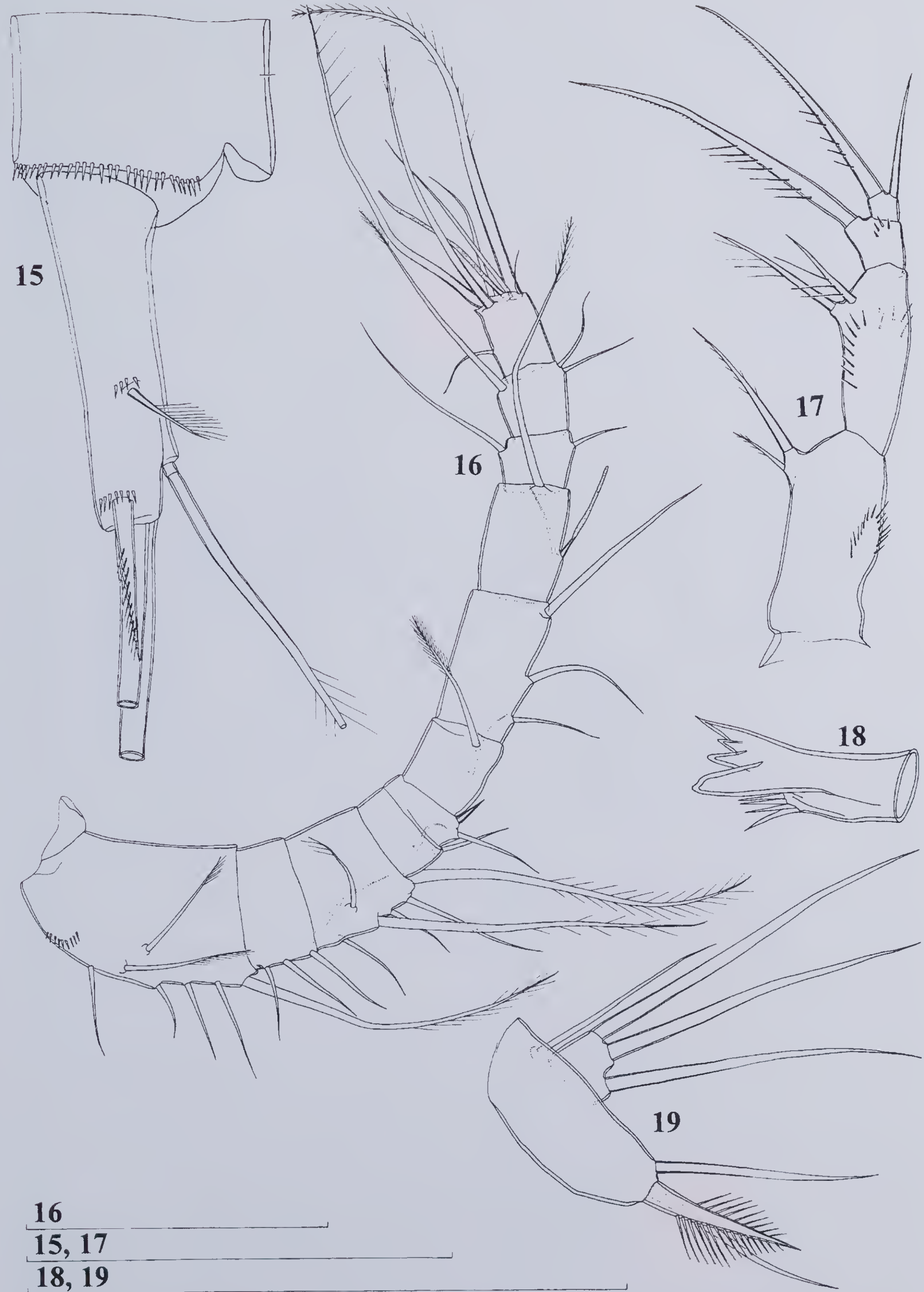
Labrum (Figure 12) trapezoidal, ornamented with 2 bunches of nearly 30 long and slender spinules on ventral surface. Cutting edge straight, with 13 relatively large teeth between produced sharp lateral corners. No other ornamentation visible.

Mandibula (Figures 7, 10 and 18) with small but distinct palp, armed with 2 very long, finely plumed setae and 1 short, smooth, seta on distal end. Coxal gnathobase cutting edge with very strong teeth and 2 outermost pinnate setae; one seta somewhat longer than neighboring tooth, other much shorter.

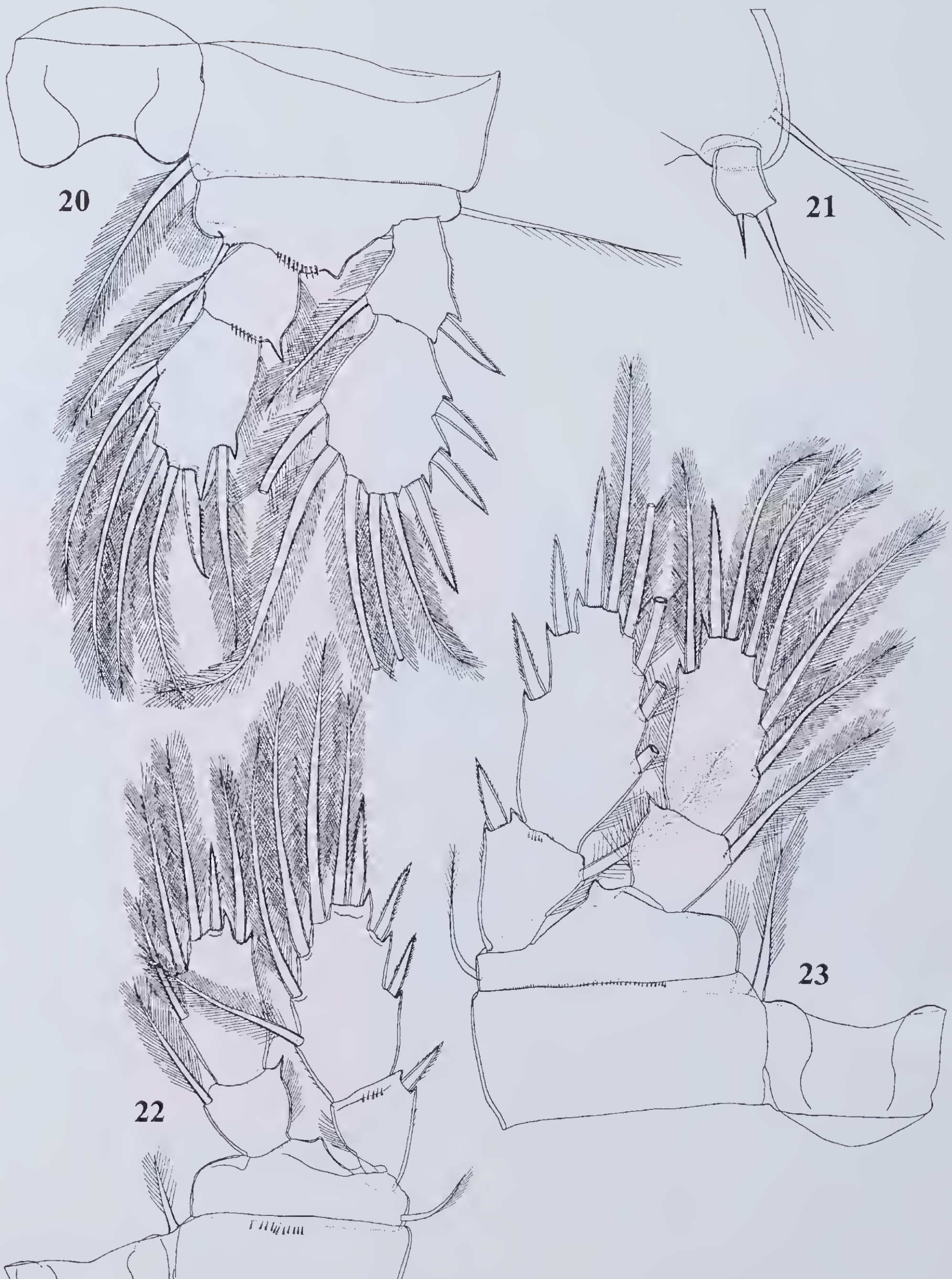
Maxillula (Figures 6 and 19) composed of well developed praecoxa and 2-segmented palp. Arthrite



Figures 9–14 *Metacyclops kimberleyi* sp. nov., holotype (female): 9 – anal somite and caudal rami, dorsal view; 10 – mandibula; 11 – fifth pedigerous and genital double-somite, lateral view; 12 – labrum; 13 – second exopodal segment of second swimming leg; 14 – sixth leg, lateral view. Scales = 0.1 mm.



Figures 15–19 *Metacyclops kimberleyi* sp. nov., holotype (female): 15 – anal somite and left caudal ramus, lateral view; 16 – antennula; 17 – maxilliped; 18 – mandibula, coxal gnathobase; 19 – maxillular palp. Scales = 0.1 mm.



Figures 20–23 *Metacyclops kimberleyi* sp. nov., holotype (female): 20 – first swimming leg; 21 – fifth leg; 22 – fourth swimming leg; 23 – third swimming leg. Scales = 0.1 mm.

of praecoxa with 4 strong apical spines; only 1 distinct and ornamented with 2 setules. Praecoxa armed with 6 armature elements along inner margin, longest one pinnate. Palp with distinct endopod, which bearing 2 apical and 1 lateral smooth setae, and armed laterally with 1 exopodal smooth seta and apically with 2 slender and smooth setae and 1 robust, strongly bipinnate, spine. Margin between endopod and distal part of basis straight.

Maxilla (Figure 8) enormous comparing with other mouth appendages, 5-segmented, but praecoxa fused to coxa on posterior surface, and also partly on anterior surface. No ornamentation visible. Proximal endite of praecoxa elongate, slender, armed with 2 pinnate setae; distal endite short, unarmed. Proximal endite of coxa with 1 bipinnate seta; distal endite highly mobile, elongate, and armed apically with 1 slender and 1 strong and bipinnate seta. Basis expanded into not very robust claw, ornamented with longitudinal row of strong spinules along concave margin (all spinules of about same length), and armed with 2 setae; strong seta as long as claw, pinnate. Endopod 2-segmented; proximal segment armed with 2 robust setae; distal segment with 1 robust and pinnate apical seta and 2 slender and smooth setae. Longest seta on distal endopodal segment slightly longer than strong seta on basis.

Maxilliped (Figure 17) 4-segmented, composed of syncoxa, basis and 2-segmented endopod. Syncoxa ornamented with arched row of spinules on proximal part of outer margin, armed with 2 bipinnate setae; distal seta almost 2.5 times as long as proximal one. Basis 2.3 times as long as wide, ornamented with 1 longitudinal and 1 transverse row of long spinules, and armed with 2 strong unipinnate setae. First endopodal segment ornamented with 4 small spinules, armed with 1 very strong, spiniform and unipinnate, seta. Second endopodal segment without any ornamentation, armed with only 2 apical setae; inner seta twice as long as outer one and 0.8 times as long as seta on first endopodal segment.

All swimming legs with 2-segmented exopods and endopods (Figures 13, 20, 22 and 23). Swimming legs armature formula as follows (legend: inner/outer spine or seta; inner/terminal/outer):

	Exopod		Endopod	
Segments	1	2	1	2
First leg	1/1	3/2/3	1/0	3/2/1
Second leg	1/1	4/2/2	1/0	4/2/1
Third leg	1/1	4/2/2	1/0	4/2/1
Fourth leg	0/1	4/2/2	1/0	3/1/1

Second exopodal segment spine formula: 3.3.3.3. Intercoxal sclerite of all swimming legs with concave distal margins, and without any ornamentation. Coxae of all swimming legs ornamented with row of spinules along posterior margin (those on fourth leg largest) and armed with plumose seta on distal inner corner (that on fist leg longest, on fourth leg shortest). Relatively slender spine inserted at inner corner of basis of first leg reaching somewhat beyond posterior margin of first endopodal segment. Outer seta on basis of first swimming leg long; those on other legs much shorter; just seta on second leg basis smooth, other setae unipinnate at distal end. All setae on endopods and exopods slender and plumose; no modified setae observed. Second endopodal segment of fourth swimming leg about 1.8 times as long as wide; only apical spine almost twice as short as segment (Figure 22).

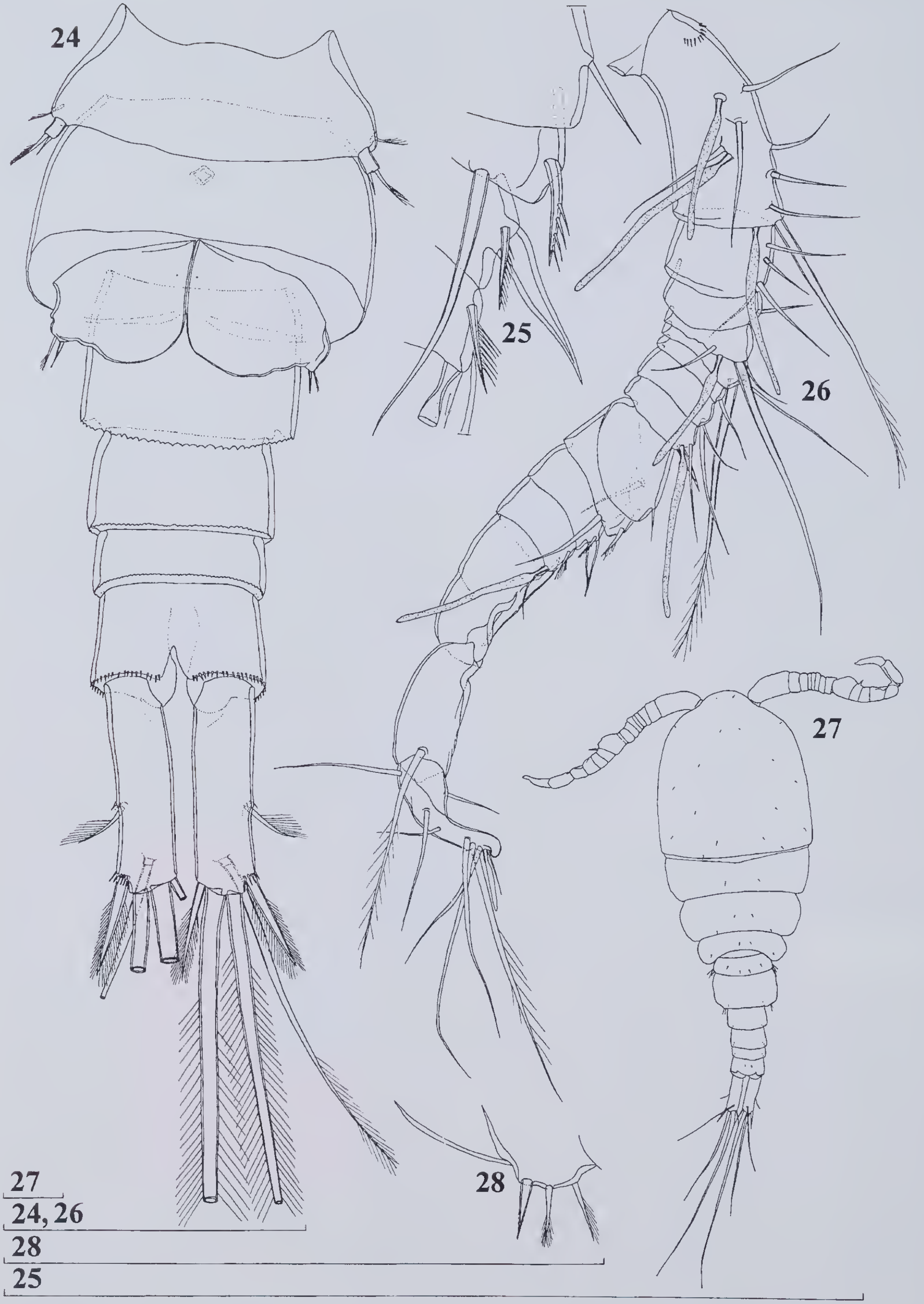
Fifth leg (Figures 2, 11 and 21) with basal segment completely fused to somite, with remnant of ancestral separation visible in dorsal view; outer basal seta inserted dorsally on somite and unipinnate at distal part. Distal segment about 1.4 times as long as wide, armed with apical outer seta and subapical inner spine; without any ornamentation. Apical seta on distal segment bipinnate at distal end, about 1.8 times as long as segment, 3 times as long as spine, and about 0.7 times as long as basal seta. Spine on distal segment smooth and 0.6 times as long as segment.

Sixth leg (Figures 2, 11 and 14) indistinct, very small cuticular plate, armed with 2 almost equal, smooth, spines, and 1 slightly longer and bipinnate seta. Median spine distinct, other one completely fused to leg.

Male (allotype). Body length, excluding caudal setae, 0.712 mm. Habitus (Figure 27) slender, with prosome/urosome ratio 1.7 and greatest width at posterior end of cephalothorax. Body length/width ratio about 2.8; cephalothorax about 2.4 times as wide as genital somite. Rostral expansion well developed. Cephalothorax slightly longer than its greatest width; represents 39% of total body length. Ornamentation of prosomal somites, colour, and nauplius eye similar to female. Hyaline fringe of fifth pedigerous somite smooth. Genital somite twice as wide as long, with irregularly serrated hyaline fringe dorsally. Hyaline fringes of other urosomal somites (except anal one) finely serrated both dorsally and ventrally. Anal somite ornamented with 2 large dorsal sensillae and with transverse row of spinules on posterior margin.

Caudal rami (Figure 24) parallel, with space between them less than half of 1 ramus width, and about 3.8 times as long as wide. Armature and ornamentation similar to female.

Antennula (Figures 25 and 26) 15-segmented (ancestral fifth and sixth, as well as sixteenth and seventeenth, segments fused), geniculate, with geniculation between thirteenth and fourteenth segments, longer than cephalothorax. First segment with 3 aesthetascs; 1 aesthetasc present on fourth,



Figures 24–28 *Metacyclops kimberleyi* sp. nov., allotype (male): 24 – urosome, ventral view; 25 – antennula, detail; 26 – antennula; 27 – habitus, dorsal view; 28 – sixth leg, lateral view. Scales = 0.1 mm.

eighth, twelfth, and fifteenth segment. All aesthetascs slender and short. Setal formula as follows: 7.4.1.2.1.2.1.2.2.2.2.2.2.1.1.3.6. Many setae characteristically modified, spiniform. Part of tenth segment as distinct lobe, bearing 1 slender and 1 spiniform seta. Elements of thirteenth and fourteenth and segments typically transformed as log T-shaped plates.

Antenna, labrum, mandibula, maxillula, maxilla, maxilliped and swimming legs similar to female. Second endopodal segment of fourth swimming leg with slightly longer apical spine than in female.

Fifth leg (Figure 24) similar to female. Distal segment about 1.5 times as long as wide, armed with apical outer seta and subapical inner spine; without any ornamentation. Apical seta on distal segment bipinnate at distal end, about 1.8 times as long as segment, twice as long as spine, and as long as basal seta. Spine on distal segment smooth and slightly shorter than segment.

Sixth leg (Figure 28) simple cuticular plate, clearly divided on outer surface, armed with 1 spine and 2 pinnate setae; ornamented with single cuticular pore. Both setae and spine of about same length.

Variability

Besides the holotype and allotype only one additional adult specimen has been collected and studied (both under brightfield compound microscope and scanning electron microscope), although not dissected. That paratype female is slightly shorter than the holotype (0.845 mm), but without any other noticable variation.

Etymology

The name is derived from the region Kimberley (Western Australia) where the species was collected. It is to be treated as a noun in the genitive singular.

Metacyclops pilbaricus sp. nov.

Figures 3 and 29–44

Material Examined

Holotype

Female (WAM C28633), Western Australia, Pilbara, Newman Borefield, groundwater monitoring bore WB 23/4, 23°19'03"S, 119°51'02"E, 23 July 1997, leg. W. F. Humphreys and S. M. Eberhard (BES 4823 and 4829): dissected on two slides.

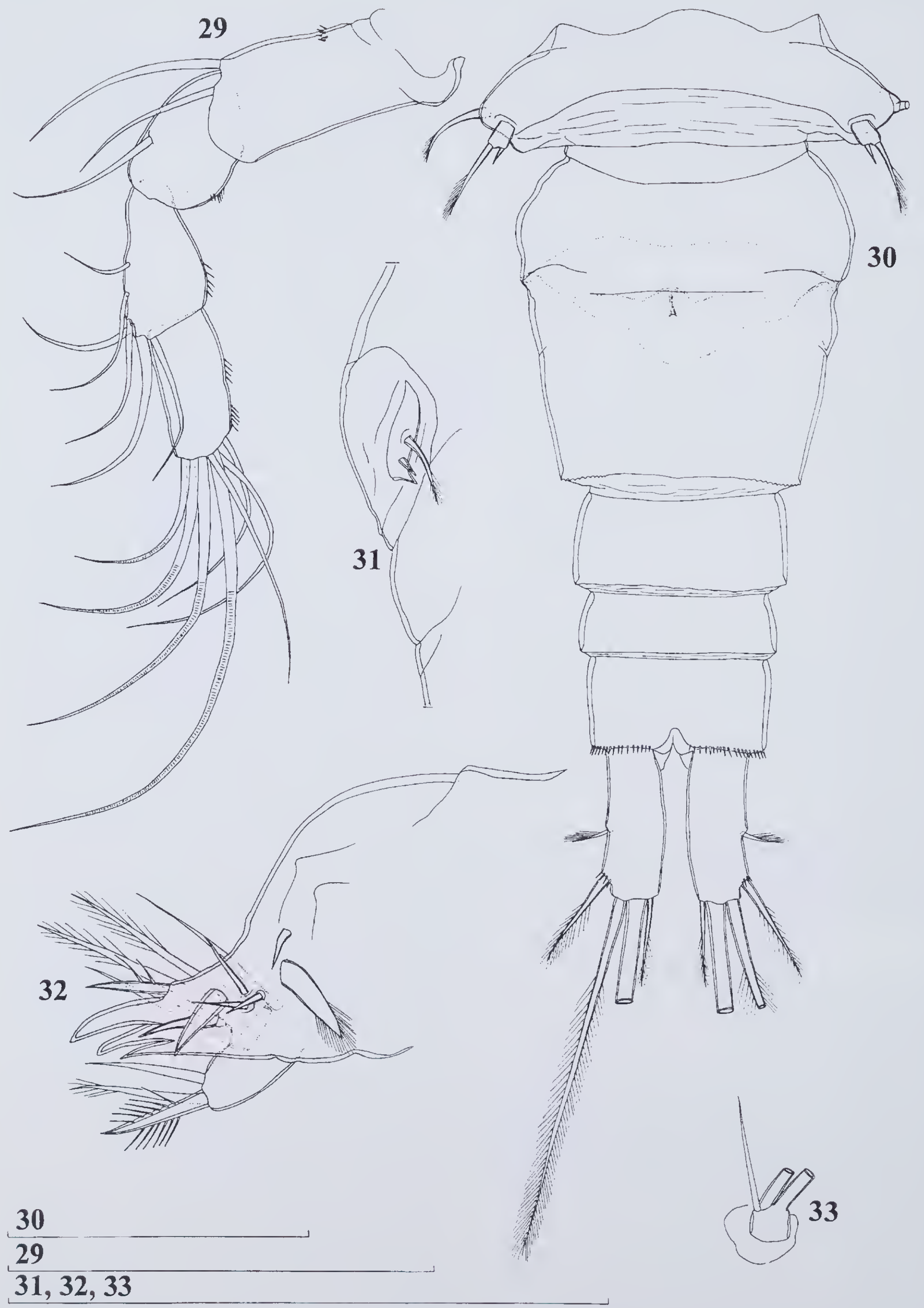
Paratypes

Western Australia, Pilbara, Newman Borefield, groundwater monitoring bore WB 23/4, 23°19'03"S, 119°51'02"E, 23 July 1997, leg. W. F. Humphreys and S. M. Eberhard (BES 4823 and 4829): two copepodids in alcohol (WAM C28634).

Description

Female (holotype). Body length, excluding caudal setae, 0.7 mm. Habitus (Figure 3) very characteristic, spindle-shaped, with prosome/urosome ratio 1.5 and greatest width at middle of cephalothorax length. Body length/width ratio about 3; cephalothorax about 2.1 times as wide as genital double-somite. Rostral expansion well developed. Free pedigerous somites without particular expansions laterally. Preserved specimen colourless. Nauplius eye not visible. Rostrum well developed, membranous, broadly rounded and furnished with two large sensillae. Cephalothorax slightly longer than wide; represents 34% of total body length. Surface of cephalothorax shield smooth, ornamented only with many large sensillae. Whole body smooth, without any cuticular pits. Hyaline fringes of prosomites narrow and smooth. Fifth pedigerous somite ornamented with 4 dorsal large sensillae; hyaline fringe smooth both dorsally and ventrally (Figure 30). Genital double-somite as long as its greatest width (ventral view), ornamented with 2 large dorsal sensillae; hyaline fringe serrated dorsally and laterally, but smooth ventrally. Copulatory pore small, squeezed and arched, situated at 2/5 of somite length; copulatory duct straight, short, well sclerotized and oriented anteriorly. Seminal receptacle relatively short but broad, represents 30% of double-somite's length, with clearly divided anterior and posterior expansions; posterior expansion approximately 1.5 times as long as anterior one (Figure 30). Ovipores situated dorsolaterally, covered with reduced sixth legs. Third and fourth urosomal somites unornamented and with smooth fringes both ventrally and dorsally; third somite about 1.5 times as long as fourth one. Anal somite with smooth, convex, anal operculum, which somewhat produced posteriorly, but not reaching posterior margin of somite; ornamented with 2 large sensillae dorsally and transverse row of small spinules on posterior margin (Figure 35). Anal sinus smooth.

Caudal rami (Figures 30 and 35) parallel, with space between them less than half of 1 ramus width, and 2.6 times as long as wide; ornamented only with few minute spinules at base of lateral and outermost apical setae. Dorsal seta relatively short, about as long as ramus, inserted at 3/4 of ramus length, uniarticulate at base and pinnate at distal part. Lateral seta arising at midlength of ramus, shorter than ramus width. Outermost apical seta stout, spiniform, about 0.7 times as long as ramus, bipinnate. Innermost apical seta about 0.7 times as long as dorsal one, and 0.8 times as long as outermost apical seta. Principal apical setae without braking planes; inner seta about 2.2 times as long as outer one, and 0.37 times as long as body length. Inner principal apical seta on right ramus with abnormality, probably as consequence of damage during postembryonic development.



Figures 29–33 *Metacyclops pilbaricus* sp. nov., holotype (female): 29 – antenna; 30 – urosome, ventral view; 31 – sixth leg, dorsal view; 32 – maxillula; 33 – mandibular palp. Scales = 0.1 mm.

Antennula (Figure 34) 11-segmented, not reaching posterior margin of cephalothorax, with slender aesthetascs on eighth and eleventh segments and setal formula as follows: 7.4.6.2.2.2.3.2.2.3.7. One apical seta on eleventh segment articulating on basal part. One seta on fifth segment spiniform and very short. Just 2 setae on first segment, 1 on third, 1 on tenth and 3 setae on eleventh segment pinnate at distal part; all other setae smooth. First segment ornamented with short semitransverse row of spinules on anterior surface; other segments with no ornamentation visible, except cuticular pits. Length ratio of antennular segments, from proximal end and along caudal margins, 1 : 0.4 : 0.6 : 0.4 : 0.2 : 0.6 : 1 : 0.9 : 0.5 : 0.7 : 0.8.

Antenna (Figure 29) 4-segmented, comprising short coxobasis and 3-segmented endopod; ornamented with longitudinal rows of minute spinules on endopodal segments. Coxobasis relatively long, ornamented also with few spinules anterior surface, armed with 2 smooth setae at distal inner corner (without seta representing exopod). First endopodal segment armed with 1 smooth seta. Second endopodal segment about 1.5 times as long as wide, armed with 6 setae (4 lateral, 1 subapical, and 1 apical). Third endopodal segment twice as long as wide, armed with 7 apical setae. All setae smooth.

Labrum (Figure 36) trapezoidal, ornamented with 2 bunches of 14 long and slender spinules on ventral surface. Cutting edge straight, with 12 relatively strong and blunt teeth between produced sharp lateral corners. No other ornamentation visible.

Mandibula (Figure 33) with small but distinct palp, armed with 2 very long, finely plumed setae and 1 short, smooth, seta on distal end. Coxal gnathobase cutting edge with very strong teeth and outermost pinnate seta, which shorter than short seta on palp.

Maxillula (Figures 32) composed of well developed praecoxa and 2-segmented palp. Arthrite of praecoxa with 4 strong apical spines; only 1 distinct and ornamented with 2 setules. Praecoxa armed with 7 armature elements along inner margin, longest one pinnate. Palp with completely divided endopod, which bearing 2 apical pinnate and 1 lateral smooth setae, and armed laterally with 1 exopodal smooth seta and apically with 2 slender setae (1 pinnate, other smooth) and 1 robust, strongly bipinnate, spine. Margin between endopod and distal part of basis without particular expansions.

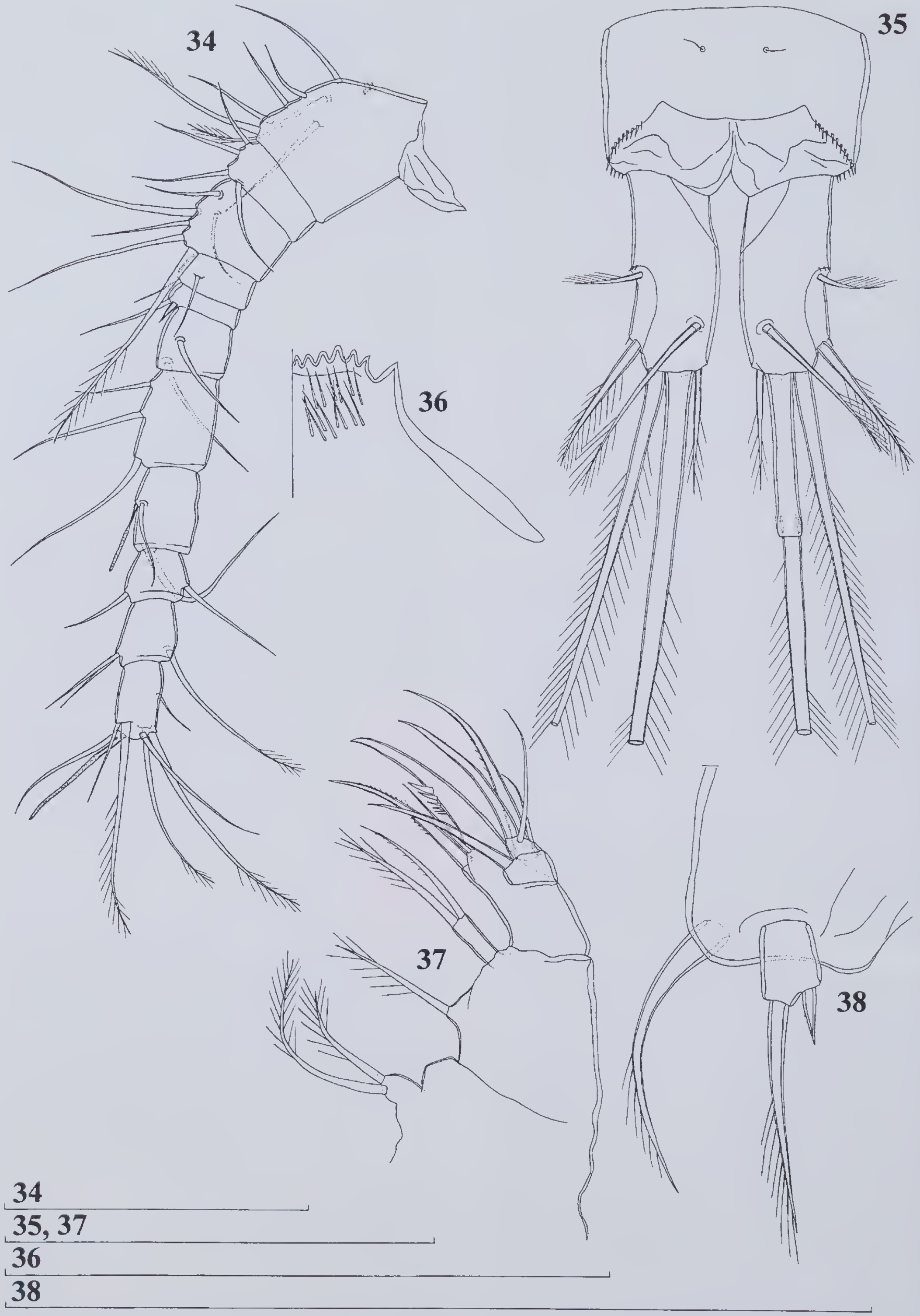
Maxilla (Figure 37) unornamented, 5-segmented, but praecoxa fused to coxa on posterior surface, and also partly on anterior surface. Proximal endite of praecoxa elongate, armed with 2 pinnate setae, distal endite small, unarmed. Proximal endite of coxa with 1 strong, bipinnate, seta; distal endite highly mobile, elongate, and armed apically with 2 subequal pinnate setae. Basis expanded into robust claw, ornamented with longitudinal row of strong spinules along concave margin (proximalmost spinules shortest), and armed with 2 setae; strong seta as long as claw, pinnate. Endopod 2-segmented; proximal segment armed with 2 robust setae; distal segment with 1 robust apical seta and 2 slender subapical setae; all setae on endopod smooth. Longest seta on distal endopodal segment as long as strong seta on basis.

Maxilliped (Figure 43) 4-segmented, composed of syncoxa, basis and 2-segmented endopod. Syncoxa ornamented with arched row of spinules on proximal part of outer margin, armed with 3 setae; middle setae strongest and longest, 1.36 times as long as proximal one, and about twice as long as distal seta; distalmost seta smooth, other 2 unipinnate. Basis 1.2 times as long as wide, ornamented with 1 longitudinal and 1 transverse row of long spinules on inner side and 1 row of spinules on outer distal corner; armed with 2 strong pinnate setae. First endopodal segment ornamented with transverse row of spinules along posterior margin; armed with 1 strong spiniform seta. Second endopodal segment without any ornamentation, armed with 2 smooth and 1 pinnate spiniform seta. Strongest seta on second endopodal segment about 1.2 times as long as seta on first endopodal segment.

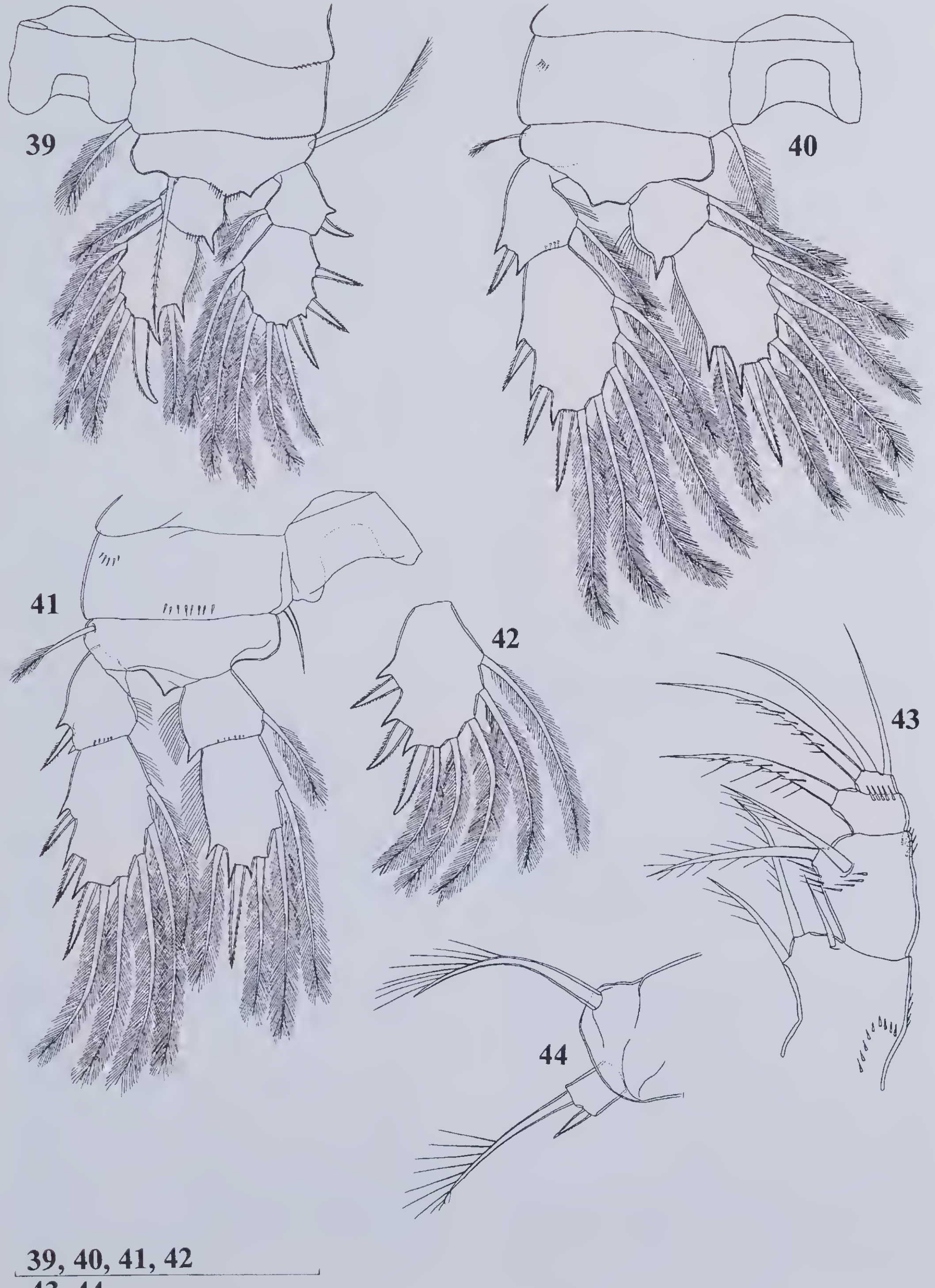
All swimming legs with 2-segmented exopods and endopods (Figures 39, 40, 41 and 42). Swimming legs armature formula as follows (legend: inner/outer spine or seta; inner/terminal/outer):

	Exopod		Endopod	
Segments	1	2	1	2
First leg	1/1	3/2/3	1/0	3/2/1
Second leg	1/1	4/2/2	1/0	4/2/1
Third leg	1/1	4/2/2	1/0	4/2/1
Fourth leg	0/1	4/2/2	1/0	3/1/1

Second exopodal segment spine formula: 3.3.3.3. Intercoxal sclerite of all swimming legs with deeply concave distal margins, and without any ornamentation. Coxa of fourth swimming leg ornamented with 2 row of spinules; coxae of other swimming legs with only 1 row of spinules each. All coxae with long and plumose seta on distal inner corner, except on fourth leg, where that seta is smooth and spiniform. Spine inserted at inner corner of basis of first leg reaching distal margin of second endopodal segment. Outer seta on basis of first swimming leg very long; those on other legs much shorter; just seta on second leg basis smooth, other setae pinnate at distal end. All setae on endopods and exopods slender and plumose; no modified setae observed. Second endopodal segment of fourth swimming leg about 1.6 times as long as wide; only apical spine about 0.85 times as long as segment (Figure 41).



Figures 34–38 *Metacyclops pilbaricus* sp. nov., holotype (female): 34 – antennula; 35 – anal somite and caudal rami, dorsal view; 36 – labrum, left half; 37 – maxilla; 38 – fifth leg, ventral view. Scales = 0.1 mm.



Figures 39–44 *Metacyclops pilbaricus* sp. nov., holotype (female): 39 – first swimming leg; 40 – third swimming leg; 41 – fourth swimming leg; 42 – second exopodal segment of second swimming leg; 43 – maxilliped; 44 – left fifth leg, dorsal view. Scales = 0.1 mm.

Figure 45 Distribution of the Australian representatives of the genus *Metacyclops*, with the proposed phyletic three of the *"trispinosus"*-group: 1 – *M. arnaudi* (Sars, 1908); 2 – *M. mortoni* Pesce, De Laurentiis and Humphreys, 1996; 3 – *M. laurentiisae* Karanovic, 2004; 4 – *M. pilanus* Karanovic, 2004; 5 – *M. superincidentis* Karanovic, 2004; 6 – *M. pilbaricus* sp. nov.; 7 – *M. kimberleyi* sp. nov. Note: one dot sometimes represents more than one locality.

Fifth leg (Figures 30, 38 and 44) with basal segment completely fused to somite, with remnant of ancestral separation visible in dorsal view; outer basal seta inserted dorsally on somite and unipinnate at distal part. Distal segment about 1.4 times as long as wide, armed with apical outer seta and subapical inner spine; without any ornamentation. Apical seta on distal segment unipinnate at distal end, about 2.7 times as long as segment, 4.2 times as long as spine, and about 0.8 times as long as basal seta. Spine on distal segment strong and 0.65 times as long as segment.

Sixth leg (Figure 31) indistinct, very small cuticular plate, armed with 2 almost equal long, smooth, spines, and 1 pinnate and much longer seta. Median spine distinct, other one completely fused to leg.

Male. Unknown.

Variability

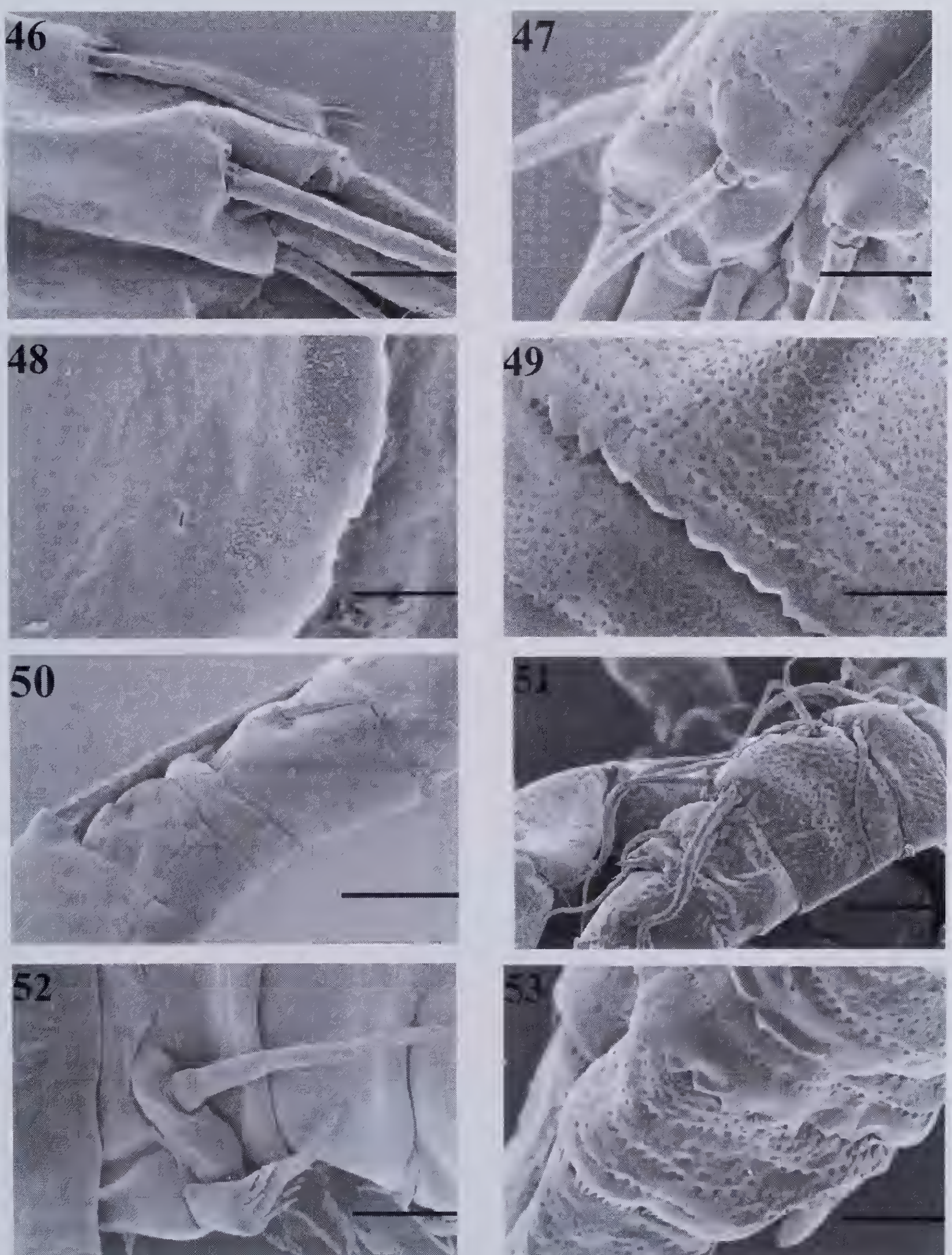
Only one female was collected and studied, and it appears to be without any significant asymmetries, apart from the abnormal inner principal apical seta on the right caudal ramus (Figure 35).

Etymology

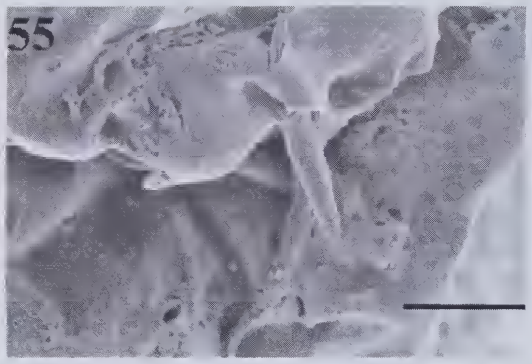
The name is derived from the region Pilbara (Western Australia) where the species was collected. It is to be treated as a latinized adjective in the nominative singular, agreeing in gender with the masculine generic name.

DISCUSSION

About 60 different species and subspecies are presently known to be members of the genus



Figures 46–53 Scanning electron micrographs of two Australian *Metacyclops*: 46 – *M. kimberleyi*, female, right caudal ramus dorsally (scale = 11 µm); 47 – *M. laurentiisae*, female, caudal rami dorsally (scale = 9 µm); 48 – *M. kimberleyi*, female, genital double–somite, posterior margin dorsally (scale = 6 µm); 49 – *M. laurentiisae*, female, genital double-somite, posterior margin dorsally (scale = 14 µm); 50 – *M. kimberleyi*, female, part of antennula (scale = 17 µm); 51 – *M. laurentiisae*, female, part of antennula (scale = 21 µm); 52 – *M. laurentiisae*, male, part of antennula (scale = 6 µm); 53 – *M. laurentiisae*, female, anal somite laterally (scale = 14 µm).



Figures 54–55 Scanning electron micrographs of *Metacyclops laurentiisae*: 54 – female, fifth leg ventrally (scale = 10 µm); 55 – female, sixth leg laterally (scale = 4.3 µm).

Metacyclops, but the real systematic position for many of those remains elusive owing to the standards of description at the time they were described (Karanovic, 2004). Many morphological features within the genus are extremely different, which raises the question as to its monophyly and validity. The antennula, for example, can be composed of nine, ten, 11, 12, or even 17 segments (although in a majority of species it is composed of 11 or 12 segments), and second endopodal segment of the fourth swimming leg can be armed apically with one or two spines, or even with just one seta, or one seta and one spine. The shape of the fifth leg also differs markedly between species, but because this appendage is very small and difficult to describe it has often been underused in species descriptions, despite its general shape being one of the main generic features (Figure 54). It is highly possible that a more detailed examination of the fifth leg, along with many other currently neglected characters, will result in splitting the genus *Metacyclops* into several different genera. Fiers (2001) took an initial step it that direction, when he transferred two Australian species into a separate new genus. Recently I have established a new genus (Karanovic, 2004) to accommodate another Australian species: *M. fiersi* De Laurentiis, Pesce and Humphreys, 2001. In contrast Plesa (1981) attempted to unite the three genera *Apocyclops* Lindberg, 1942, *Psammophilocyclops* Fryer, 1956, and *Metacyclops* Kiefer, 1927, as subgenera of the genus *Metacyclops*, but without sufficient justification (see Reid, 1987; Karanovic, 1999). A proper revision of the genus *Metacyclops*, with careful reexamination (especially details of the antennulae, antennae and mouth appendages armature) and redescription of many species is certainly needed before phylogenetic studies can be conducted.

However, one group of species seems to be not only an easily recognizable morphological group, but a phyletic group as well. It has a clear Eastern Gondwana connection (Africa, India, Australia and New Zealand) and I named it the "*trispinosus*"-group (Karanovic, 2004) after *M. trispinosus* Dumont, 1981, because this species' name contains the main distinguishing character: only three spines on the second exopodal segment of all the swimming legs. Besides the African *M. trispinosus*, which was described by Dumont (1981), the "*trispinosus*"-group also includes the following five species: *M. arnaudi* (Sars, 1908) from Australia (Sars, 1908); *M. laurentiisae* Karanovic, 2004 also from Australia (Karanovic, 2004); *M. margaretae* (Lindberg, 1938) from India (Lindberg, 1938); *M. monacanthus* (Kiefer, 1928) from New Zealand (Kiefer, 1928); and *M. pilanus* Karanovic, 2004 from Australia. The new species described in the present paper also belong to this group, which means that Australia is the centre of diversity (with five out of eight species), although this could be a collecting bias. Two apical spines on the endopod of the fourth swimming leg is a symplesiomorphy of the African *M. trispinosus* and Indian *M. margaretae*, which also share relatively short and subequal principal apical setae on the caudal rami. Both these species are surface water inhabitants (see Lindberg, 1938; Dumont, 1981). All other species of the "*trispinosus*"-group have an apomorphic endopod of the fourth leg, with just one apical spine. They are all Australian species, except *M. monacanthus* which was described from the Lake Ellesmere near Christchurch in New Zealand (Kiefer, 1928). This latter species is also a surface water inhabitant and is only partially described. Unfortunately, we know nothing about its antenna or mouth appendages, although I believe they are very similar to those of *M. arnaudi* since Kiefer (1928) wrote: "*Cyclops monacanthus* nov. spec. besitzt eine auffallende, ohne Zweifel auf Verwandtschaft beruhende Ähnlichkeit mit *C. arnaudi* Sars". However, a detailed redescription of this species is necessary before it can be further discussed phylogenetically.

Of the five Australian species of the "*trispinosus*"-group, only one, *M. arnaudi*, is a surface water inhabitant. As previously mentioned, this species was described from a swamp at St. Arnaud in Victoria by Sars (1908). It is morphologically very similar, and probably phylogenetically very close, to two sympatric subterranean species from the Murchison Region: *M. laurentiisae* and *M. pilanus*. They all share a plesiomorphic antenna morphology, with the exopod present and the second endopodal segment with the full armature (nine setae). As depicted on the proposed phyletic tree for the "*trispinosus*"-group (Figure 45) I assume that *M. arnaudi* has separated earlier from the common ancestor than *M. laurentiisae* and *M. pilanus*, but this may not necessarily be the case and probably only an molecular analysis could give us a more accurate answer. These three species can be distinguished from each other only by details in their habitats and caudal rami shape. The two new species, on the other hand, have an antenna without an exopod and the second endopodal segment with only six setae, which is a synapomorphy that separates them at once from the three other representatives of this group in Australia. *Metacyclops kimberleyi* sp. nov. is distinguished from other members of the group by at least two autapomorphies: the exceptionally long dorsal seta on caudal rami (Figure 9) and the maxilliped with only seven armature elements (Figure 17). It differs from *M. pilbaricus* sp. nov. also by the habitus shape from dorsal view (Figures 1 and 3), seminal receptacle (Figures 4 and 30), caudal rami shape (Figures 9 and 35) and the fifth leg (Figures 21 and 38). *Metacyclops kimberleyi* has enormous maxillae (Figure 8), which extend far away from the body, although there is nothing unusual in the morphology of these conservative appendages other than their size. This may be one of the preadaptations for a predatory way of life, which may be further supported by its robust habitus and large body (for a subterranean species) and also by the morphology of the maxilliped, which is equipped with fewer but much stronger setae and looks like a more powerful grasping organ than in other members of the "*trispinosus*"-group. *Metacyclops pilbaricus* can be distinguished from each member of the group by a number of characters, but the only clear autapomorphy of this species is its unusual body shape (Figure 3), which is more harpacticoid-like (without very obvious distinction between prosome and urosome). It should be also noted here that both *M. kimberleyi* and *M. pilbaricus* have a very smooth surface of all somites and appendages (Figures 46, 48 and 50), while *M. laurentiisae* and *M. pilanus* have numerous cuticular pits (Figures 46, 49, 51 and 53). The situation of this character is not known in *M. arnaudi*. Although there is little doubt that the five Australian representatives of the "*trispinosus*"-group share a common ancestor, the phylogenetic position of this group within the genus *Metacyclops*, as well as the position of the other two Australian *Metacyclops*, is currently unclear. These questions are not always easy to answer even in groups where we have a full set of morphological, physiological, behavioral, ecological and molecular characters, so they would need to wait until at least a proper morphological revision of the genus *Metacyclops* can be presented.

As the genus *Metacyclops* in Australia already has seven valid species, a key to aid in their identification is presented below as well as a map of their distributions (Figure 45).

Key to the Australian *Metacyclops* species

1. Swimming legs with second exopodal segment spine formula 3.3.3.3 3
   Spine formula different 2
2. Spine formula 3.4.4.3 .... *M. superincidentis* Karanovic, 2004
   Spine formula 3.4.4.2 .... *M. mortoni* Pesce *et al.*, 1996
3. Exopod of antenna present; second endopodal segment with 9 setae 4
   Exopod of antenna absent; second endopodal segment with 6 setae 6
4. Caudal rami not more than 4 times as long as wide 5
   Caudal rami about 7 times as long as wide .... *M. arnaudi* (Sars, 1908)
5. Dorsal seta on caudal ramus shorter than outermost apical one .... *M. laurentiisae* Karanovic, 2004
   Dorsal seta longer than outermost apical one .... *M. pilanus* Karanovic, 2004
6. Dorsal seta on caudal ramus about as long as ramus .... *M. pilbaricus* sp. nov.
   Dorsal seta more than twice as long as ramus .... *M. kimberleyi* sp. nov.

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First record of a neolampadoid echinoid from the Paleogene of Western Australia

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Abstract – A neolampadoid echinoid is described from the Late Eocene Pallinup Limestone, western Eucla Basin. This represents the first record of this order from the Paleogene of the western half of the continent. The echinoid is characterised by the possession of a tetrabasal apical system that has only two gonopores. It shares many similarities with *Aphanophora*? *bassoris* Holmes, 1995, from the coeval Kingscote Limestone, Kangaroo Island, South Australia, with which it is questioningly compared. The only record of a living species of *Aphanophora* found in Australian waters is based on a single neolampadoid collected from northwestern Australia, and tentatively assigned to the genus. The temporal range of this genus in the eastern Indian Ocean region may therefore extend back some 40 million years to the Late Eocene.

INTRODUCTION

Four species of neolampadoid echinoids have been described from the Cenozoic of Australia. The oldest of these are *Pisolampas concinna* Philip, 1963 and *Aphanophora*? *bassoris* Holmes, 1995, both of which been found within late Middle to early Late Eocene units deposited during the Tortachilla Transgression, in the St Vincent Basin in southeastern Australia. The former species was described on the basis of material collected from the Tortachilla Limestone, which outcrops at the southern end of Maslin Bay, South Australia, the latter from the lower beds of the Kingscote Limestone, Kangaroo Island, South Australia. The other two species, found in the St Vincent, Murray and Otway Basins are: *Notolampas flosculus* Philip, 1963, from the Late Oligocene? to Early Miocene Gambier Limestone, Mannum Formation and Port Willunga Formation in South Australia, and *Actapericulum bicarinatum* Holmes, 1995, from the Early Miocene Puebla Formation in Victoria, and the Mannum Formation and Gambier Limestone in South Australia (Holmes 1995).

Here we describe a single specimen of a neolampadoid echinoid from the Pallinup Formation in the western Eucla Basin. The specimen represents the first record of this order of echinoids from Paleogene deposits in the western half of the continent. Neolampadoid echinoids have been recorded, though not described, from the Neogene of the Eucla Basin. Specimens of *Notolampas* have been collected from the eastern part of the Eucla Basin, where they are said to occur in the Early Miocene Abrakurrie Limestone (Holmes 1995). There is also an unsubstantiated record of a specimen referred to as *Pisolampas* sp. nov. by Philip (1970) occurring in this same formation (Holmes 1995).

The Late Eocene Pallinup Formation, within which the neolampadoid occurs, outcrops in the western part of the Eucla Basin (formerly the Bremer Basin) (Clarke *et al.* 2003). It is a unit of spongolite and siltstone that contains a small, but distinctive, echinoid fauna. The unit has been correlated with planktonic foraminiferal zone P15 (Late Eocene), and represents part of the Tuketja Transgression across southern Australia (Clarke *et al.* 2003). The Pallinup Formation forms part of the Plantagenet Group, and overlies the Late Eocene Werillup Formation. This formation, deposited within the Tortachilla Transgression, overlies the late Middle Eocene Nanarup Limestone, which also contains a distinctive echinoid fauna (Martin & McNamara in prep.).

Few echinoids have been recorded from the Pallinup Formation. However, McNamara (1985) has described the spatangoid *Linthia pulchra*; and McNamara *et al.* (1986) recorded the spatangoid *Gillechinus cudmorei* Fell, 1964. Unlike other echinoid faunas from the Eucla Basin, the Pallinup Formation echinoids are invariably preserved as internal and external moulds. The specimen under consideration is, to our knowledge, unique for this formation in that it occurs as a chalcedonic internal mould. While external plate details are missing, the plate boundaries are exceptionally well preserved (Fig.

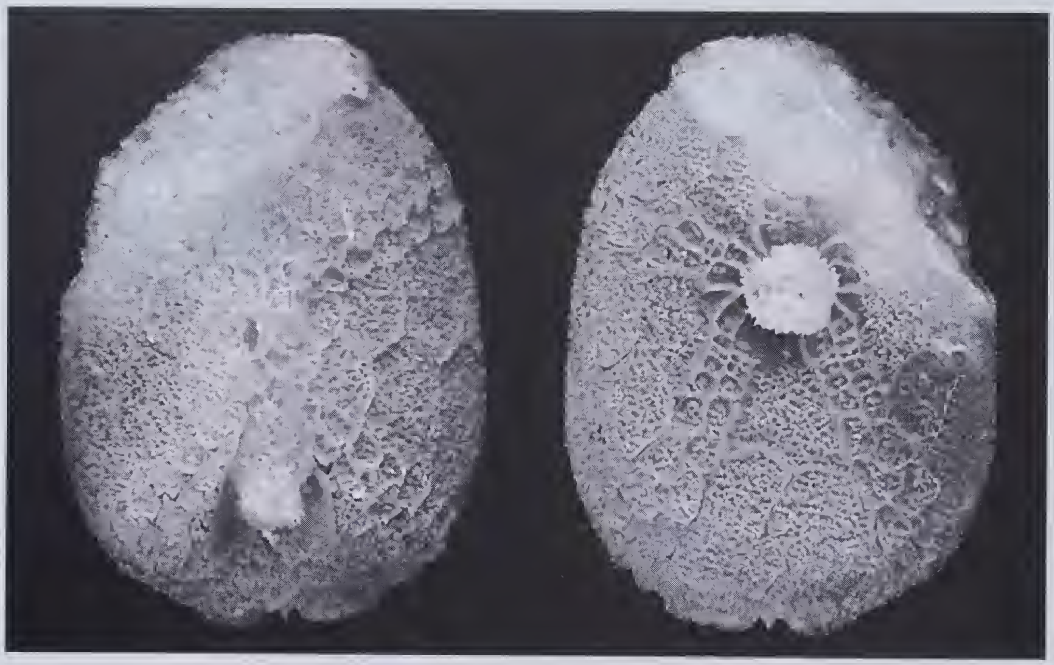
A B

Figure 1 *Aphanophora*? cf. *bassoris* Holmes, 1995, WAM 65.7, Pallinup Formation, Lort River, Western Australia; A, adapical view; B, adoral view; both x11.5.

1). Gonopores are also preserved by being infilled with single crystals of quartz, the 'c' axes of which are perpendicular to the plane of the test.

The echinoid fauna of the Pallinup Formation is dominated by spatangoids, including *Linthia pulchra* McNamara, 1985, *Gillechinus cudmorei* Fell, 1964, ?*Hemiaster* sp., *Schizaster* cf. *tatei* McNamara and Philip 1980, *Prenaster* cf. *aldingensis* Hall 1907 and ?*Pericosmus* sp. The cidaroid ?*Stereocidaris* is also present.

Test parameters are expressed as %TL, which refers to a measurement as a percentage of test length. Other measurements are in millimetres, measured under an optical microscope with calibrated graticule.

SYSTEMATIC PALAEONTOLOGY

Order Neolampadoida Philip, 1963

Suborder Neolampadina Philip, 1963

Family Neolampadidae Lambert, 1918

Genus *Aphanophora*? de Meijere, 1903

Aphanophora? cf. *bassoris* Holmes, 1995

Figures 1–3

Material

One siliceous internal mould, WAM 65.7, from "the Plantagenet Group". The specimen is recorded as having been collected from "Lort River", west of Esperance, Western Australia. Other material held in the collections of the Western Australian Museum from the Lort River region was collected from close to where the river intersects the Albany-Esperance Road, suggesting the echinoid may be from the same vicinity. The other fossils collected from the Lort River area are molluscs, sponges and nautiloids and are characteristic of the Pallinup Formation. Moreover, there is no Werillup Formation preserved in the Lort River region (Thom *et al.* 1977), supporting the view that the test was derived from the Pallinup Formation. The nature of preservation, as an internal siliceous mould, rather than the original test, is also suggestive of derivation from this unit. Overall, the specimen is well preserved, with the exception of an incomplete anterior.

Description

Test elongate, elliptical, 8.2mm long, tapering slightly towards posterior. Maximum width 75%TL, occurring 59%TL from anterior. Test low, maximum height of 50%TL at around mid-test. Ventral surface

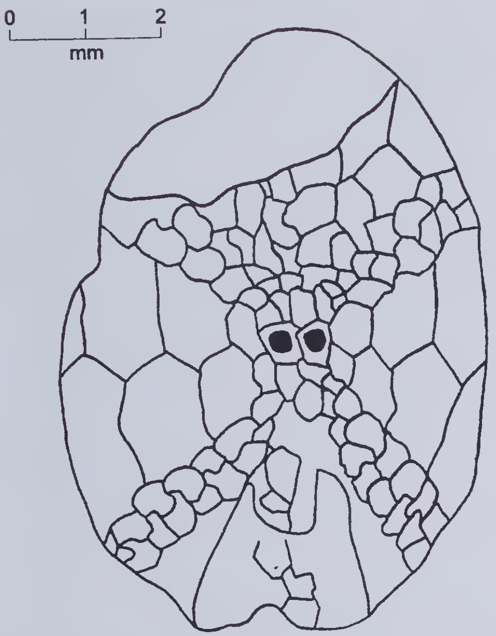

Figure 2 Adapical plating of *Aphanophora*? cf. *bassoris* Holmes, 1995, WAM 65.7, Pallinup Formation, Lort River, Western Australia. Anterior section not preserved.

concave around peristome. In lateral profile region between apex and posterior margin is steeper and flatter than gently curved area anterior of apical system. Ambitus rounded, with exception of a slight indentation on the posterior margin caused by anal groove. No anterior notch (Figures 1,2).

Apical system anterior of apex, and 49%TL from test anterior; tetrabasal, with two gonopores (Figures 2, 3); these occur in genital plates 1 and 4 and are large (diameter = 6%TL) and closely spaced. No hydropores preserved. Pore pairs not apparent. Anterior ambulacra diverge at 110°; posterior ambulacra at 75°. No demiplates visible adapically, although ambulacral plates appear to become more irregular in shape adambitally.

Periproct lies on adapical surface within an anal groove and on an angle of around 45° to ventral surface. Anal groove relatively wide; length about 25% TL. Periproct rounded, longer than wide and inset well into the adapical surface. Periproct length 15%TL, width 10%TL. Anterior anal groove edge lies 73%TL from anterior.

Peristome a little sunken within adoral surface; rounded, and slightly wider than long (Figure 1B). Peristome dimensions difficult to determine. Anterior margin lies 38%TL from anterior ambitus; surrounded by small bourrelets; phyllodes biserial with regular rows of single pores. No demiplates visible within phyllodes; no buccal pores observed. Primary tubercles not preserved.

Remarks

Despite the absence of the test, the nature of the preservation of this specimen as an internal mould is such that the salient features required for its likely generic assignment are mainly preserved. These include, particularly, the tetrabasal apical system; presence of only two gonopores; adapical periproct situated in anal groove; and apparent absence of pore pairs in the adapical ambulacra. During his study of the Cenozoic species of neolampadoids from southern Australia, Holmes (1995) argued that a form from the Late Eocene Kingscote Limestone was distinct from the other three species in possessing a tetrabasal, rather than a monobasal, apical system and only two gonopores, both characteristics of the Pallinup Formation specimen. *Pisolampas* and *Notolampas* have three gonopores and *Actapericulum* four. Rather than assigning the Kingscote Limestone form to a new genus, Holmes questioningly assigned it as a new species within the living genus *Aphanophora*. The author of the genus, de Meijere (1903) did not provide a separate generic diagnosis in the original description, although he did in a subsequent paper (de Meijere 1904). This, as Holmes (1995) points out, shows a close concordance of characters between the Kingscote Island specimen and the modern form. However, neither de Meijere nor Mortensen (1948) provided any information on the nature of apical system. For this reason Holmes only questioningly assigned his form to the new taxon *Aphanophora bassoris*.

The Pallinup Formation specimen is very similar to the Kingscote Limestone species in most features.

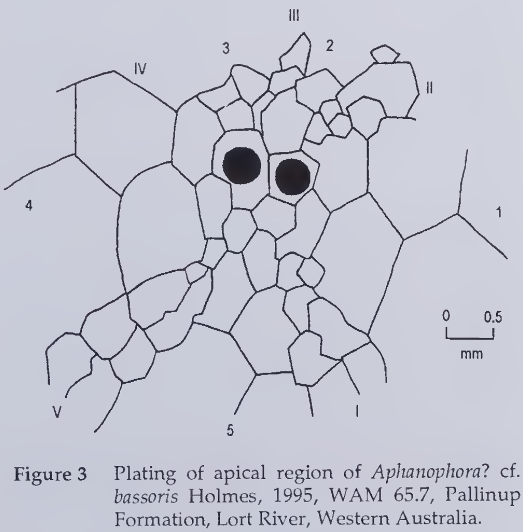

Figure 3 Plating of apical region of *Aphanophora*? cf. *bassoris* Holmes, 1995, WAM 65.7, Pallinup Formation, Lort River, Western Australia.

Table 1 Comparison of *Aphanophora*? cf. *bassoris* Holmes, 1995 from the Pallinup Formation with *A.*? *bassoris* from the Kingscote Limestone. TL=test length; TW=test width; TH=test height; Ant. amb.=anterior ambulacrum; PS=peristome; PP=periproct; PPL=periproct length; PPW=periproct width.

	Pallinup Fm	Kingscote Limestone*
TL (mm)	8.2	7.5–11.0
Max TW %TL	75	86.9–93.4
TW from ant. %TL	59	52.4–63.2
Max TH %TL	50	47.6–59.3
TH from ant. %TL	50	49.5–63.6
No. of gonopores	2, large	2, large or small
Apical from ant. %TL	49	43.7–53.5
Adapical ant. amb °	110	127
Adapical post. amb °	75	76
PS from ant. %TL	38	37.8–43.1
PPL %TL	15	–
PPW %TL	10	4.9–13.6
PP from ant. %TL	73	66.0–77.8
Posterior test angle °	45	46

*Data from Holmes (1995) and Holmes (pers. com. 2004)

These include test length, test height, gonopore number, position of apical system, divergence of posterior adapical ambulacra, position of peristome, periproct width and angle of test surface close to periproct (see Table 1). The only significant differences between the two forms are the test width and angle of divergence of the anterior petals. The Pallinup Formation form has an appreciably narrower test (75%TL vs 86.9–93.4%TL) and less divergent anterior petals (110° vs 127°). Although there is probably a slight difference in ages between the Kingscote Limestone, which was deposited during the older Tortachilla Transgression, and the Pallinup Formation, which was deposited during the younger Tuketja Transgression, these two morphological differences are unlikely to be of sufficient significance to warrant the erection of new species.

DISCUSSION

A single specimen of a neolampadoid is known from the waters off the Western Australian coast. The 13.5 mm long, 10.8 mm wide specimen (WAM 97.1037) was dredged off the northwestern Australian coast at a depth of 324 m from moderately sorted, muddy sand at 23°18.18'S, 113° 08.65'E. McNamara (1998) suggested that this specimen may be referred to *Aphanophora*.

A.? cf. *bassoris* from the Pallinup Formation differs from WAM 97.1037 in being relatively narrower (75%TL compared with 80%TL) and having a less rounded posterior margin. However, both share some of the characteristic features of *Aphanophora*, notably the absence of pore pairs in the adapical ambulacra and supramarginal periproct. In both specimens weak bourelets are developed around the peristome. Unfortunately, the apical system of the living form is missing, thus it cannot be assigned to *Aphanophora* with certainty either.

It is interesting to note that, apart from *A.*? cf. *bassoris* from the Pallinup Formation, all the other neolampadoids from the Cenozoic of southern Australia occur exclusively in calcarenites (Holmes 1995). Although occurring in a much finer grained unit, the silty spongolites of the Pallinup Siltstone are considered to have been deposited in relatively shallow water, close to the shore line (Gammon *et al.* 2000). Today *Aphanophora* occurs in depths of 350–390m (McNamara 1998), suggesting that during the Cenozoic this neolampadoid has migrated from a relatively shallow, nearshore habitat, to a deeper, outer shelf environment.

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Ants of the southern Carnarvon Basin, Western Australia: An investigation into patterns of association

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Abstract – A study of the ant species of the southern Carnarvon Basin was carried out in order to identify the patterns of species distribution and associations across a transitional landscape. The study yielded 35 genera and 243 species of ants, 58% of which were positively identified and the remaining placed into species complexes. Twelve assemblages of associated species were found, with members having a predominantly arid zone biogeographic distribution, with some southern elements. The suggestion by Gibson *et al.* (2000) to push the boundary of the South-west Province more south and west was supported by the ant species in this study, as there were more arid zone affinities in two southern sites of the study area. Species assemblages were positively associated with temperature, rainfall, longitude and altitude, but genus assemblages yielded a more latitudinal association.

Key words: Ant species, ant genera, species associations, biogeographic origin.

INTRODUCTION

Biological inventorying and monitoring is an important part of environmental management; it allows those involved to make responsible decisions regarding biodiversity and ecosystem functioning (Stork and Samways 1995). Incorporation of biodiversity survey data with geographical data should provide the basis for understanding broad-scale patterns across ecosystems, while at the same time establishing comprehensive databases for flora and fauna. These databases could then be utilized in environmental assessment procedures, in rapid biodiversity assessment studies and to provide support for gazetting areas for conservation (Greenslade 1985, McKenzie *et al.* 1989, Kremen *et al.* 1993, Oliver and Beattie 1993, Stork and Samways 1995).

Invertebrates are increasingly being incorporated into biological surveys as they play major roles in ecosystem functioning (McGeoch 1998). Often, due to the scale of invertebrate collections, indicator or surrogate taxa are chosen for facilitating rapid assessment of environments (Oliver and Beattie 1996, Lawton *et al.* 1998). Ants are often selected as they are easily collected and are involved in a variety of ecosystem functions (Alonso 2000), such as seed dispersal (Drake 1981); predator-prey interactions (Rossbach and Majer 1983); nutrient cycling (Greenslade and Thompson 1981); and in the maintenance of soil quality (Lobry De Bruyn 1999). Studies on the patterns of their distribution can contribute to a better understanding of the biogeographic characteristics of the environment within which they live (Fisher 1999).

The Australian ant fauna has been noted as one of the most complex groups in Australia and has also been ranked as one of the richest known ant faunas in the world (Greenslade and Greenslade 1989, Andersen and Burbidge 1992, Andersen 1993, Shattuck 1999). Out of the 21 subfamilies recognised in the world (Bolton 2003), 13 are found in Australia, containing 100 genera, and 1275 described species (Shattuck 1999), with at least as many again undescribed species (Majer *et al.* 2004). This abundance of species identifies ants as a major influence in the functioning of any habitat.

Comprehensive studies of the Western Australian (WA) ant fauna have been carried out in some regions of the State, but the information available remains fragmented. To date, due to a paucity of research in many areas of WA, a thorough list or map of species occurrences is unavailable. Studies of Australia's arid zone have revealed high species richness compared to arid zones in other regions of the world (Morton 1982, Andersen 1997). Also, research in specific regions such as the semi-arid areas to the south, has demonstrated a great diversity of species (Andersen and Burbidge 1992). This indicates that WA should be home to a large diversity of ants, as the arid zone in the north and, semi-arid areas to the south cover a large percentage of it.

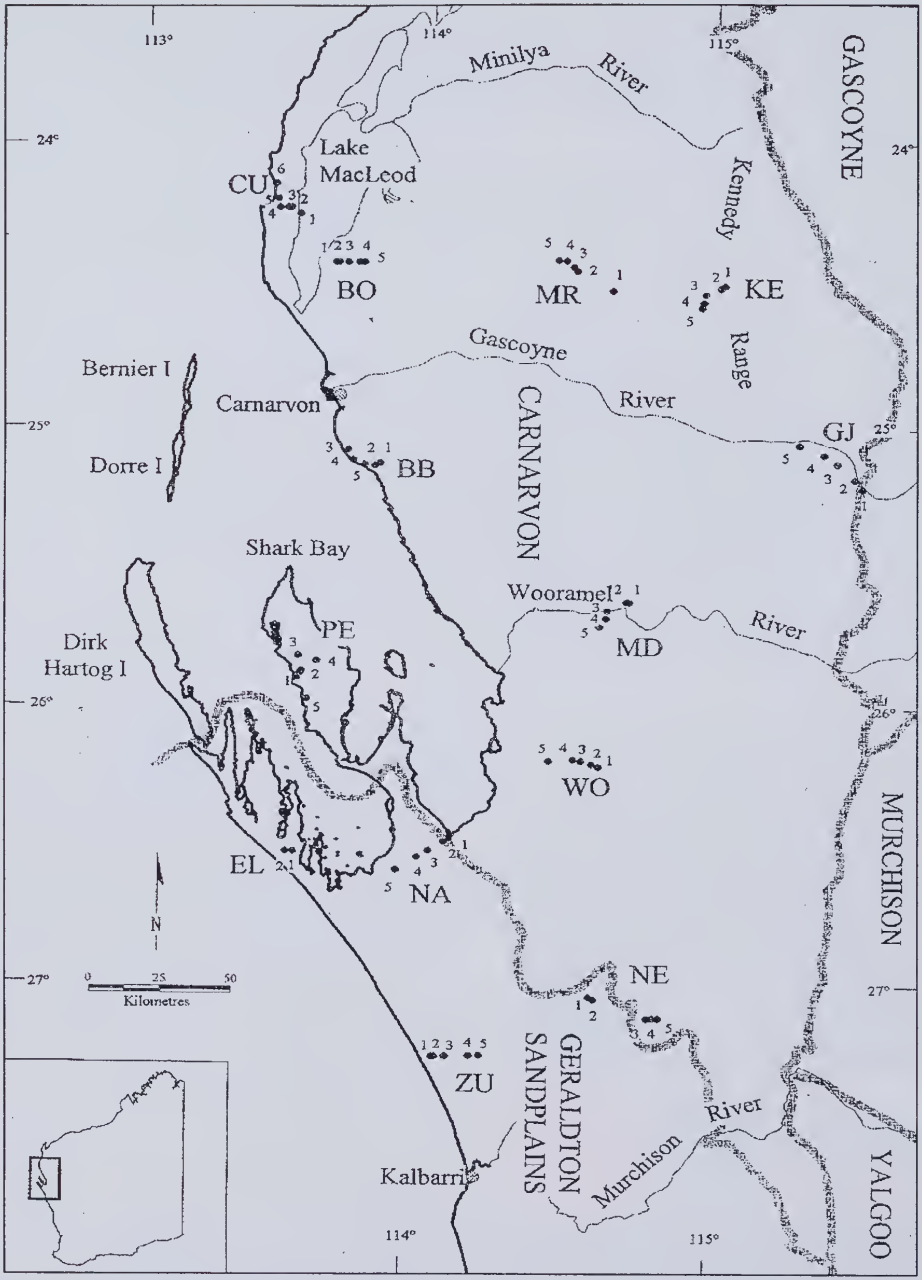


Figure 1 Map of the southern Carnarvon Basin study site, displaying the 13 survey areas and their corresponding quadrats that were investigated during the survey. Edel Land (EL) was the only area not included in the current study. The map also shows the major geographic boundaries that traverse the region.

Preliminary studies in and around the Carnarvon Basin suggest a highly diverse biota. However, until Environment Australia (EA), the Department of Conservation and Land Management (DCLM) and the Western Australian Museum (WAM) jointly carried out the comprehensive faunal and floristic study of the southern Carnarvon Basin, there was no survey that combined climatic and geological variables with biotic factors such as vegetation and invertebrate distribution. The 13 sites chosen for the study were largely distributed around the southern portion of the Basin, which included the crossover

Table 1 Brief characteristics of the vegetation groups (Keighery *et al.* 2000).

Vegetation group	Quadrat	General characteristics
1-4	BB; BO; CU; GJ; KE3-5; MD; MR1-2, 4-5; NA 1-2; PE1-4; WO	Coastal and inland *Acacia* shrublands interspersed with *Eucalyptus* or *Melaleuca* woodlands.
5-6	KE1-2; MR3; NE1, 3-5; PE5	*Eucalyptus-Callitris* woodlands or *Eucalyptus-Acacia* woodland
7	NE2	*Banksia* woodland
8-9	NA3-5; ZU	*Eucalyptus* woodland

zones for the Eremaean and South-western Provinces (Burbidge *et al.* 2000). The book that resulted from this study included chapters on climate, geology, flora, various vertebrate groups and invertebrate groups such as spiders and centipedes.

This paper documents the ant species in the southern Carnarvon Basin (SCB) for 12 of the 13 sites, identifies species assemblages, and investigates how these relate to the geomorphologic and climatic variables in this region. It represents the first thorough inventory of ants in a transitional zone from the northern to the southern fauna, and contributes to a better understanding of the distributions and associations of the WA ant fauna.

METHODS

Study area

The ant species were collected as part of a large comprehensive floristic and faunal study carried out in a 75, 000 km^2 region of WA. The study area extended from the Cape Range in the Exmouth area (near the Minliya River) outwards to the Kennedy Range and Gascoyne Junction, with a southern extension to the Murchison River (Figure 1). The study area includes the Interim Biogeographic Regionalisation of Australia (IBRA) regions of the Geraldton Sand plains and the Carnarvon Region. The whole study area traverses Beard's South-western phytogeographic province (SWBP) in the south and the Eremaean province to the north (Burbidge *et al.* 2000).

These boundary areas represent the meeting of the arid and southern mesic areas of WA. The DCLM and WAM chose this area for their surveys in order to supplement and improve the knowledge of the patterns of distribution of plants and animals in this highly varied and ecologically significant system (Burbidge *et al.* 2000). In view of the high degree of variability within the region, 13 study sites were positioned in a stratified random array, stretching from Cape Cuvier to the north to the Zuytdorp cliffs in the south. The sites incorporated the typically northern *Acacia* shrub lands and the southern *Eucalyptus* woodlands and heaths, interspersed with hummock and tussock grasslands upon low dunes along the coastline (Keighery *et al.* 2000). These sites were coded as: BB- Bush Bay; BO- Boolathana; CU- Cape Cuvier; EL- Edel Land; GJ- Gascoyne Junction; KE- Kennedy Range; MA- Mardathuna; MD- Meedo; NA- Nanga; NE- Nerren Nerren; PE- Peron Peninsula; WO- Woodleigh; and ZU- Zuytdorp (Figure 1).

Each survey area contained five quadrats. Two exceptions were CU, which had six quadrats and EL, which had only two. For the ant study, only 12 survey areas were analysed, as the samples from EL were unavailable. Each quadrat contained five traps, totalling 305 traps altogether.

Vegetation

The vegetation study conducted by Keighery *et al.* (2000) revealed nine major vegetational groups (Table 1). The vegetation assemblages of groups 1–4 were the most species-rich and widespread across the study area. There was a high saline influence within the plots in group 1 (quadrats BB1, BB3, BO2, CU1 and PE2), with a number of *Halosarcia* and *Atriplex* species, which are saline-adapted. Group 6 differed from group 5 in that these quadrats were located on top of the Kennedy Range (MR3, KE1 and KE2). Group 7 was hypothesized to be a transitional zone between the *Eucalyptus* woodlands of group 5 and the limestone heaths of group 9 (Keighery *et al.* 2000). The last two groups, differed from each other in that group 8 had *Eucalyptus* woodlands over red dunes (NA 3–5), whereas group 9 (ZU1–5) was woodland over a limestone heath.

Climate and geomorphology

The climate of the region also reflects the variability in the landscape. Lying in a transitional region, the area is affected by the typical winter rainfall patterns of the southwest, as well as the monsoonal summer conditions of the north (Wyrwoll *et al.* 2000a). Geological and geomorphological patterns are described in Wyrwoll *et al.* (2000b) and are briefly characterised in Table 2. Ten regions and morphological features traverse the study area. Further details of each individual quadrat are described in Wyrwoll *et al.* (2000b).

Field sampling

Invertebrate pitfall traps were placed at 13 sites throughout the study area. Two types of pitfall

Table 2 General geological and geomorphological patterns of each survey area (Wyrwoll *et al.* 2000b).

Survey Area	Geomorphological features
CU and BO	All quadrats in CU and BO were located in the MacLeod Region, comprised of marine and aeolian alluvial sediments. The main morphological feature is Lake MacLeod, characterised by a number of linear calcareous sand dunes and tidal flats.
BB and GJ	The Carnarvon Coastal Plain includes BB1-5 and GJ2-5 together. Although the sites are located on opposite sides of the study area, they are found to the south of the Gascoyne River, in the alluvial deposition of the Gascoyne River deltas. GJ1 sits outside this area in the Bidgemia Region furthest inland of all the sites.
KE	The Kennedy Region includes all quadrats of KE and is characterised by extensive scree slopes around the plateau, cotnaining some of the largest sand dunes in the area.
MR	Quadrats MR2-5 fell into the Mardathuna Regions- mainly dune covered calcrete areas with associated coastal and riverine settings. MR1 falls into the more noncalcareous gradational soils of the Binthalya Region.
NA and PE	Sites NA1-5 and PE1-5 are placed in the Peron Region, located in and around the coast of the Peron Peninsula. Linear dunes traverse the large undulating sand plains of the area with interdunal corridors containing evaporite pans (birridas).
MD, NE, WO and ZU	The Victoria Plateau includes a variety of sites; these are MD4-5, NE1-5, WO 1-2, ZU3-5 and all generally characterised by gently undulating sand plains and small dune fields. The Wooramel Region (MD1-3) is transitional between the Carnarvon Region and the Carbla Plateau. It has soils associated with the drainage valley of the Wooramel River. The Carbla plateau (WO3-5) has well-developed limestone ridges that are similar to the Edel Region, containing EL1-2 and ZU1-2. The difference in the Edel Region is the type of limestone, which in this case is Tamala limestone with more yellow rather than red sands dominating the dune formations

traps were used. 'Wet' traps were 25 L buckets (300mm diameter x 400 mm depth) dug into the ground, with the rim flush with the ground surface. Five 10 cm holes were then cut into the lids and a piece of chicken wire placed below the lid to allow vertebrates to escape. Each bucket contained approximately 3.5 L of a mix of ethylene glycol, formalin (1%) and water (10%). Five traps were placed at 5m intervals along a transect at each quadrat. The traps were left open for one year from August 1994 to August 1995 and were cleared three times (September, January and May) prior to the final clearance at the end of the trapping period. All the samples were returned to the laboratory to be cleaned and stored in 75% ethanol (Harvey *et al.* 2000).

'Dry' traps used to collect vertebrate fauna were located in the same quadrats but were slightly smaller (125mm diameter x 500mm depth) and were connected by flywire drift fences (McKenzie *et al.* 2000). Two 5-day trapping efforts in September 1994 and May 1995 yielded a number of invertebrate samples as the traps were cleared daily during the 5-day period. All samples from these traps were stored in 75% ethanol. All ant species were removed and sorted to species level. The species were then identified in the laboratory and restored to their permanent storage units. All specimens are lodged in the WAM collection, and vouchers of each species are lodged in the Curtin University of Technology Ant Collection.

The preserved samples available were the October 1994 wet trap collection, October 1994 dry trap collection and July 1995 dry trap collection. Samples from the other collection periods (January, May and August 1995) and from the EL survey area were not available from WAM. Species that could not be positively identified to species level were placed into species complexes and assigned Australian National Insect Collection (ANIC) numbers or Curtin University Ant Collection (JDM) numbers for future identification.

Data analysis

All ant species were recorded as being either present or absent at any particular trap. Species occurrences from the wet and dry trap types were combined, as differences in sampling efforts could not be quantified. Only presence/absence data were analysed, as analyses of relative abundances of ant species are often problematic due to the tendency of the data to be spatially clumped and biased as a result of differences in sampling method and effort (Longino 2000). All species that occurred at only one quadrat ('uniques') were removed due to the uncertainty of whether these species were not caught by the sampling method or as a result of their actual rarity.

Biogeographic affiliations

Each species' biogeographic affiliation was determined using distribution criteria based on previous collections of the ant species across WA and Australia. In the case of new species, affiliations

Table 3 List of all ant species collected and identified in the 1994-1995 southern Carnarvon Basin survey and their biogeographic distribution. Some species are listed under more than one biogeographic region due to uncertainty of their origin or because their range traverses more than one region. Species have been listed as widespread if they occur in all three biogeographic regions. #Indicates new species to Curtin University Ant Collection.

Subfamily	Species	Southern	Arid	Tropical	Widespread
Myrmeciinae	*Myrmecia callima* (Clark)		*		
	Myrmecia desertorum Wheeler	*	*		
	Myrmecia elegans (Clark)	*	*		
	Myrmecia?elegans (Clark) #		*		
	Myrmecia hilli (Clark)		*		
	Myrmecia urens gp. JDM sp. 1	*			
	Myrmecia nr. *urens* gp. JDM sp. 71	*			
	Myrmecia urens gp. JDM sp. 728	*			
	Myrmecia ?varians Mayr #	*	*		
	Myrmecia sp. nr *pilosula* Smith		*		
Cerapachyinae	*Cerapachys brevicollis* (Clark)	*			
	Cerapachys brevis (Clark)				*
	Cerapachys clarki (Crawley)	*			
	Cerapachys fervidus (Wheeler)				*
	Cerapachys gilesi (Clark)	*			
	Cerapachys greavesi (Clark)	*			
	Cerapachys incontentus Brown		*		
	Cerapachys sjostedti Forel	*	*		
	Cerapachys JDM sp. 741		*		
	Cerapachys JDM sp. 1049		*		
	Cerapachys JDM sp. 1103	*			
Ponerinae	*Anochetus armstrongi* MacAreavy	*	*		
	Leptogenys clarki Wheeler				*
	Leptogenys darlingtoni Wheeler		*		
	Leptogenys nr. *tricosa* JDM sp. 1021 Taylor			*	
	Odontomachus ruficeps Smith				*
	Pachycondyla denticulata gp. JDM sp. 730		*		
	Pachycondyla lutea (Mayr)				*
	Pachycondyla piliventris regularis Forel		*		
	Rhytidoponera crassinoda (Forel)		*	*	
	Rhytidoponera dubia gp. JDM sp. 904		*		
	Rhytidoponera foveolata Crawley	*	*		
	Rhytidoponera metallica (Smith)				*
	Rhytidoponera metallica gp. JDM sp. 1097		*		
	Rhytidoponera metallica gp. JDM sp. 1098 #		*		
	Rhytidoponera micans Clark		*		
	Rhytidoponera taurus (Forel)		*	*	
	Rhytidoponera tyloxys Brown and Douglas		*	*	
	Rhytidoponera violacea (Forel)				*
	Rhytidoponera JDM sp. 736		*		
Myrmicinae	*Anisopheidole antipodum* (Smith)	*			
	Aphaenogaster barbigula Wheeler	*			
	Colobostruma cerornata Brown	*	*		
	Crematogaster cornigera gp. JDM sp.126				*
	Crematogaster dispar Forel	*			
	Crematogaster frivola Forel		*		
	Crematogaster queenslandica gp. JDM sp. 428	*			
	Crematogaster queenslandica gp. JDM sp. 1099			*	
	Crematogaster queenslandica gp. JDM sp. 1100			*	
	Crematogaster JDM sp. 859	*	*		
	Epopostruma quadrispinosa (Forel)		*		
	Meranoplus dichrous Forel		*		
	Meranoplus fenestratus Smith	*			
	Meranoplus JDM sp. 74				*
	Meranoplus JDM sp. 423	*	*		
	Meranoplus JDM sp. 424	*			
	Meranoplus JDM sp. 679		*		
	Meranoplus JDM sp. 866	*			
	Meranoplus JDM sp. 1071		*		

Table 3 (cont.)

Subfamily	Species	Southern	Arid	Tropical	Widespread
Myrmicinae (cont.)	*Meranoplus* JDM sp. 1101		*		
	Monomorium aithoderum Heterick	*	*		
	Monomorium anthracinum Heterick	*			
	Monomorium disetigerum Heterick		*	*	
	Monomorium eremophilum Heterick		*		
	Monomorium fieldi Forel				*
	Monomorium laeve Mayr				*
	Monomorium leae Forel	*	*		
	Monomorium legulus Heterick		*		
	Monomorium nanum Heterick	*	*		
	Monomorium rothsteini Forel				*
	Monomorium rufonigrum Heterick	*	*		
	Monomorium silaceum Heterick			*	
	Monomorium sordidum Forel				*
	Monomorium striatifrons Heterick		*		
	Monomorium sydneyense Forel				*
	Monomorium whitei Wheeler		*		
	Pheidole ?bos Forel (JDM sp. 164)	*	*		
	Pheidole deserticola Forel		*		
	Pheidole hartmeyeri Forel	*	*		
	Pheidole nr. *variabilis* JDM sp. 177 Mayr				*
	Pheidole JDM sp. 338		*		
	Pheidole JDM sp. 558	*			
	Pheidole JDM sp. 681		*		
	Podomyrma adelaidae (Smith)				*
	Podomyrma christae (Forel)	*	*		
	Solenopsis belisarius Forel	*			
	Solenopsis clarki Crawley	*			
	Strumigenys quinquedentata Crawley	*	*		
	Tetramorium impressum (Viehmeyer)				*
	Tetramorium sjostedti Forel		*	*	
	Tetramorium spininode Bolton		*		
	Tetramorium striolatum Viehmeyer				*
	Tetramorium nr. *striolatum* Viehmeyer	*			
	Tetramorium viehmeyeri Forel	*			
	Tetramorium JDM sp. 461		*		
	Tetramorium JDM sp. 515	*			
	Tetramorium JDM sp. 884	*	*		
	Tetramorium JDM sp. 1007		*		
	Tetramorium JDM sp. 1072	*	*		
Dolichoderinae	*Bothriomyrmex flavus* Crawley	*			
	Bothriomyrmex JDM sp. 232	*			
	Doleromyrma darwiniana (Forel)	*			
	Dolichoderus formosus Clark	*			
	Dolichoderus glauerti Wheeler	*			
	Dolichoderus JDM sp. 838		*		
	Iridomyrmex agilis Forel		*		
	Iridomyrmex agilis gp. JDM. sp. 85	*			
	Iridomyrmex bicknelli Emery				*
	Iridomyrmex bicknelli azureus Viehmeyer		*		
	Iridomyrmex bicknelli brunneus Forel				*
	Iridomyrmex cephaloinclinus Shattuck		*		
	Iridomyrmex chasei Forel				*
	Iridomyrmex chasei concolor Forel				*
	Iridomyrmex discors Forel	*			
	Iridomyrmex dromus Clark				*
	Iridomyrmex exsanguis Forel				*
	Iridomyrmex greensladei Shattuck	*			
	Iridomyrmex hartmeyeri Forel		*		
	Iridomyrmex hartmeyeri gp. JDM sp. 327		*	*	
	Iridomyrmex lividus Shattuck		*		
	Iridomyrmex mattiroloi continentis Forel		*	*	
	Iridomyrmex mattiroloi splendens Forel	*			

Table 3 (cont.)

Subfamily	Species	Southern	Arid	Tropical	Widespread
Dolichoderinae (cont.)	*Iridomyrmex mattiroloi* complex JDM sp. 449	*			
	Iridomyrmex reburrus Shattuck			*	
	Iridomyrmex rufoniger suchieri Forel	*			
	Iridomyrmex rufoniger suchieri complex JDM sp.390	*	*		
	Iridomyrmex nr. *rufoniger suchieri* JDM sp. 314 Forel	*	*		
	Iridomyrmex sanguineus Forel			*	
	Iridomyrmex viridiaeneus Viehmeyer		*		
	Iridomyrmex JDM sp. 130		*		
	Iridomyrmex JDM sp. 133	*			
	Iridomyrmex JDM sp. 319		*		
	Iridomyrmex JDM sp. 597			*	
	Iridomyrmex JDM sp. 843		*		
	Iridomyrmex JDM sp. 846		*		
	Iridomyrmex JDM sp. 1028		*	*	
	Ochetellus glaber gp. JDM sp. 19				*
	Ochetellus JDM sp. 851	*	*		
	Papyrius nitidus (Mayr)	*			
	Tapinoma JDM sp. 78				*
	Tapinoma JDM sp. 981				*
Formicinae	*Calomyrmex glauerti* Clark	*			
	Calomyrmex ANIC sp. 1	*			
	Camponotus arcuatus Mayr		*		
	Camponotus ?arcuatus gp. JDM sp. 694		*		
	Camponotus capito ebenithorax Forel	*	*		
	Camponotus chalceus Crawley	*			
	Camponotus cinereus Mayr	*	*		
	Camponotus cinereus amperei Forel		*		
	Camponotus clarior Forel		*		
	Camponotus claripes Mayr				*
	Camponotus claripes minimus Crawley	*	*		
	Camponotus claripes gp. JDM sp. 63	*			
	Camponotus claripes gp. JDM sp. 229	*			
	Camponotus nr. *claripes* complex JDM sp. 767	*			
	Camponotus claripes complex JDM sp. 779	*	*		
	Camponotus claripes gp. JDM sp. 939		*		
	Camponotus claripes gp. JDM sp. 1073	*	*		
	Camponotus discors Forel			*	
	Camponotus discors complex JDM sp. 309	*			
	Camponotus cf. *discors* complex JDM sp. 1104		*		
	Camponotus dromas Santschi		*		
	Camponotus dryandrae McArthur and Adams	*			
	Camponotus ephippium gp. JDM sp. 598		*		
	Camponotus gasseri (Forel)				*
	Camponotus gibbonotus Forel				*
	Camponotus gouldianus Forel		*		
	Camponotus lownei Forel				*
	Camponotus lownei complex JDM sp. 179	*	*		
	Camponotus lownei complex JDM sp. 761	*			
	Camponotus lownei complex JDM sp. 772		*		
	Camponotus novaehollandiae gp JDM sp. 144			*	
	Camponotus nigroaeneus gp nr JDM sp. 108	*			
	Camponotus oetkeri Forel				*
	Camponotus prosseri Shattuck and McArthur	*	*		
	Camponotus prostans Forel	*			
	Camponotus rufus Crawley	*			
	Camponotus scratius Forel	*			
	Camponotus tasmani Forel		*		
	Camponotus terebrans (Lowne)	*			
	Camponotus tricoloratus Clark		*	*	
	Camponotus whitei Wheeler				*
	Camponotus wiederkehri Forel		*	*	
	Camponotus wiederkehri gp. JDM sp. 924	*			
	Camponotus JDM sp. 26	*			
	Melophorus nr. *aeneovirens* JDM sp. 545 (Lowne)		*	*	

Table 3 (cont.)

Subfamily	Species	Southern	Arid	Tropical	Widespread
Formicidae	*Melophorus bagoti* Lubbock		*	*	
(cont.)	*Melophorus bruneus* McAreavey	*	*		
	Melophorus bruneus complex JDM sp. 472		*		
	Melophorus bruneus complex JDM sp. 791	*			
	Melophorus bruneus complex JDM sp. 951	*			
	Melophorus curtus Forel			*	
	Melophorus insularis Wheeler				*
	Melophorus iridescens gp. JDM sp. 1034		*		
	Melophorus ludius sulla Forel		*	*	
	Melophorus mjobergi Forel				*
	Melophorus turneri Forel				*
	Melophorus turneri perthensis Wheeler				*
	Melophorus wheeleri Forel		*	*	
	Melophorus wheeleri complex JDM sp. 783	*			
	Melophorus wheeleri complex JDM sp. 1077		*		
	Melophorus ANIC sp. 3 (JDM 59)				*
	Melophorus JDM sp. 176				*
	Melophorus JDM sp. 199		*		
	Melophorus ?JDM sp. 470		*		
	Melophorus JDM sp. 500	*			
	Melophorus JDM sp. 532		*	*	
	Melophorus JDM sp. 618		*		
	Melophorus JDM sp. 699		*		
	Melophorus JDM sp. 784		*		
	Melophorus JDM sp. 787		*		
	Melophorus JDM sp. 1063		*		
	Melophorus JDM sp. 1070	*	*		
	Melophorus JDM sp. 1102	*			
	Melophorus JDM sp. 1105 #			*	
	Notoncus capitatus Forel		*		
	Notoncus gilberti Forel	*			
	Opisthopsis haddoni rufoniger Forel		*	*	
	Opisthopsis rufithorax Emery	*			
	Paratrechina minutula (Forel)				*
	Paratrechina minutula gp. JDM sp. 916		*		
	Plagiolepis squamulosa Wheeler	*			
	Polyrachis ammonoeides Roger	*			
	Polyrachis gravis Clark				*
	Polyrachis macropa Wheeler		*	*	
	Polyrachis nr. *macropa* Wheeler		*	*	
	Polyrachis schwiedlandi complex JDM sp. 1010		*	*	
	Polyrachis sidnica complex JDM sp. 390	*			
	Polyrachis cf. *sidnica* complex JDM sp. 671	*	*		
	Polyrachis (*Campomyrma*) JDM sp. 118	*	*		
	Polyrachis (*Campomyrma*) JDM sp. 670		*		
	Polyrachis (*Campomyrma*) JDM sp. 703		*	*	
	Polyrachis (*Campomyrma*) JDM sp. 805		*		
	Polyrachis (*Campomyrma*) JDM sp. 901		*		
	Stigmacros aemula (Forel)				*
	Stigmacros pilosella (Viehmeyer)		*		
	Stigmacros reticulata Clark	*	*		
	Stigmacros spinosa McAreavy		*	*	
	Stigmacros termitoxena Wheeler		*	*	
	Stigmacros JDM sp. 188	*			
	Stigmacros JDM sp. 341				*
	Stigmacros JDM sp. 1067	*	*		

were based on distribution patterns apparent from the current study. The terms used were – **southern**, for species occurring in the SWBP; **arid zone**, for ants in this study not found in the SWBP; and **tropical**, for ants that are also found in the tropical regions of WA. Ants were listed as **widespread** if they fell into all three of the above categories. It should be stressed that these categories do not

represent formal biogeographic origins of the species; they are provided to give an indication of the possible origin of the SCB fauna.

Numerical and statistical analyses

Distribution of the ant species was analysed in two ways. The first investigated the co-occurrence of species at any one quadrat using a 'two-step' association measure (Belbin 1980). The second method looked at ant species composition in each quadrat compared with every other quadrat using a Czekanowski association measure. The relationships between the species and the quadrats were then displayed as dendrograms using the 'unweighted pair group arithmetic averaging' (UPGMA) hierarchical clustering strategy (Sneath and Sokal 1973). From these dendrograms, a clustering parameter was identified and a two-way table constructed to show the assemblages of ants in relation to the groups of quadrats.

Relationships between physical and biological variables were explored to determine environmental factors that were significantly associated with ant species distribution. Eleven climatic variables recorded from ANUCLIM (McMahon *et al.* 1995) and 17 soil and geomorphic attributes were derived from sub-samples collected at a depth of 5–10 cm from 20–30 regularly dispersed points at each quadrat. Kruskal-Wallis K-sample tests were used to explore relationships between the species assemblages and the environmental variables. All data were analysed using PATN, a numerical analysis program developed to show patterns in species distribution (Belbin 1993).

Species data for individual quadrats were bulked within each survey area and analysed to explore patterns of ant composition that may have been clouded by the quadrat analysis. This was then repeated for genera to expose any differences between species and genus analyses. The same two-step procedure was utilised, resulting in dendrograms showing groups of survey areas with similar species and genus compositions.

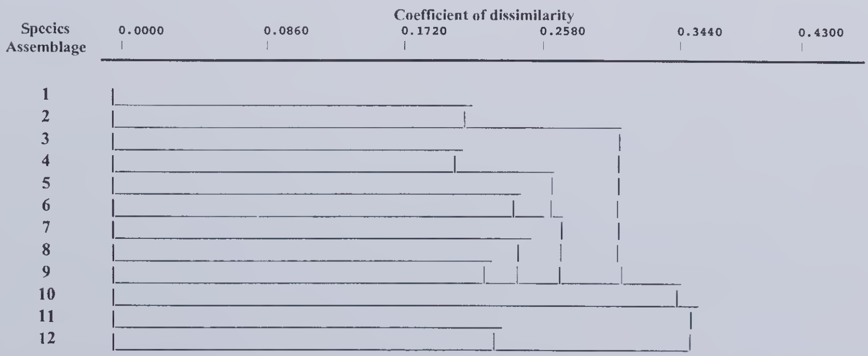
The survey area groups were compared to environmental factors using the same Kruskal-Wallis tests mentioned above. Eleven of the 17 climatic variables and 4 geographic variables (latitude, longitude, altitude and distance from the coast) were averaged for each survey area and utilised. The remaining soil and geomorphologic factors were deemed too variable to average for each survey area and were not used in the analysis.

RESULTS

Species identification

The study yielded 35 genera and 243 species of ants (Table 3) producing ant species new to the Curtin University Ant Collection and range extensions for a number of ants previously not thought to be in WA or formerly thought to be confined to the SWBP. Fifty eight percent of the species could be positively identified, with the remaining placed into species complexes and assigned ANIC or JDM numbers.

The most speciose genus was *Camponotus*, with 42 species, while *Iridomyrmex* and *Melophorus* followed close behind, with 31 and 30 respectively. *Melophorus ludius sulla* was the most ubiquitous ant, as it was found at 40 of the 61 quadrats studied, though it was not present at any BB quadrat. Three species of *Iridomyrmex* (*I. chasei*, *I. chasei concolor* and *I. dromus*) and two other *Melophorus* species (*M.* ANIC sp. 3 and *M.* JDM sp. 176) were some of the more common ants but *Camponotus gibbonotus* was the only species found at all 12 survey areas.



Species Assemblage	S	A	T	W
1	16	30	20	**34**
2	**38**	25	0	**38**
3	21	**50**	29	0
4	33	**50**	8	8
5	**43**	**57**	0	0
6	31	**50**	13	6
7	33	**44**	6	17
8	**50**	**50**	0	0
9	33	33	17	17
10	32	**58**	11	0
11	**50**	**50**	0	0
12	**56**	31	6	6

Figure 2 Dendrogram showing ant species assemblages according to similarity of distribution. The percentages of species in each phytogeographical region for each of the 12 assemblages are also displayed. Percentages greater than 33% are highlighted and used to depict the predominant biogeographic affiliations of each assemblage (**S** = southern, **A** = arid zone, **T** = tropical, **W** = widespread).

Table 4 List of all species that occurred at only one quadrat throughout the whole study area. The location of each quadrat is shown in Figure 1. These species were considered 'unique' and were not included in any analyses of data as it cannot be determined whether their occurrence in a particular quadrat was accidental (tourist) or whether the species was actually found in the area (resident).

Subfamily	Species	Quadrat	Subfamily	Species	Quadrat
Myrmeciinae	*Myrmecia elegans*	NE3	Dolichoderinae	*Iridomyrmex rufoniger suchieri* complex JDM sp. 390	CU2
	Myrmecia ?elegans	NE4	(cont.)	*Iridomyrmex* nr. *rufoniger suchieri* JDM sp. 314	NE4
	Myrmecia hilli	KE2		*Iridomyrmex* JDM sp. 843	GJ4
	Myrmecia urens gp. JDM sp. 1	CU5	Formicinae	*Camponotus arcuatus*	MR3
	Myrmecia nr. *urens* gp. JDM sp. 71	ZU3		*Camponotus ?arcuatus* gp. JDM sp. 694	CU5
	Myrmecia urens gp. JDM sp. 728	ZU3		*Camponotus capito ebenithorax*	KE4
	Myrmecia sp. nr *pilosula*	PE5		*Camponotus chalceus*	ZU2
Cerapachyinae	*Cerapachys* JDM sp. 741	WO3		*Camponotus cinereus amperei*	NE4
	Cerapachys JDM sp. 1049	MD5		*Camponotus* nr. *claripes* complex JDM sp. 767	KE4
	Cerapachys JDM sp. 1103	NA5		*Camponotus claripes* complex JDM sp. 779	MR5
Ponerinae	*Leptogenys* nr. *tricosa* JDM sp. 1021	MR5		*Camponotus claripes* gp. JDM sp. 939	MD3
	Pachycondyla denticulata gp. JDM sp. 730	NE1		*Camponotus claripes* gp. JDM sp. 1073	BO3
	Rhytidoponera dubia gp. JDM sp. 904	BB1		*Camponotus discors* complex JDM sp. 309	CU2
	Rhytidoponera metallica gp. JDM sp. 1097	NA3		*Camponotus dromas*	NE5
	Rhytidoponera JDM sp. 736	KE3		*Camponotus dryandrae*	KE3
Myrmicinae	*Anisopheidole antipodum*	NA4		*Camponotus ephippium* gp. JDM sp. 568	NE2
	Crematogaster cornigera gp. JDM sp.126	NE1		*Camponotus gasseri*	ZU2
	Epopostruma quadrispinosa	MD3		*Camponotus gouldianus*	BB2
	Meranoplus dichrous	BB1		*Camponotus lownei* complex JDM sp. 179	PE2
	Meranoplus fenestratus	NE5		*Camponotus novaehollandiae* gp JDM sp. 144	MD3
	Meranoplus JDM sp. 423	MR5		*Camponotus prostans*	BO5
	Meranoplus JDM sp. 866	NA4		*Camponotus whitei*	NE2
	Meranoplus JDM sp. 1071	NA4		*Camponotus wiederkehri* gp. JDM sp. 924	KE1
	Monomorium aithoderum	NA3		*Camponotus* JDM sp. 26	NE3
	Monomorium anthracinum	BB3		*Melophorus bruneus* complex JDM sp. 791	MD4
	Monomorium silaceum	MD3		*Melophorus curtus*	MR3
	Monomorium whitei	BB1		*Melophorus iridescens* gp. JDM sp. 1034	MD1
	Pheidole JDM sp. 338	MR3		*Melophorus* JDM sp. 532	GJ1
	Pheidole JDM sp. 681	KE3		*Melophorus* JDM sp. 618	KE3
	Podomyrma adelaidae	ZU3		*Melophorus* JDM sp. 787	NE1
	Podomyrma christae	NE1		*Melophorus* JDM sp. 1070	GJ3
	Strumigenys quinquedentata	CU6		*Melophorus* JDM sp. 1105	NE4
	Tetramorium nr. *striolatum*	WO5		*Opisthopsis rufithorax*	NE4
	Tetramorium JDM sp. 1072	KE4		*Papyrius nitidus*	ZU5
Dolichoderinae	*Bothriomyrmex flavus*	ZU2		*Polyrachis* nr. *macropa*	GJ4
	Bothriomyrmex JDM sp. 232	NA3		*Polyrachis* (*Campomyrma*) JDM sp. 118	ZU1
	Dolichoderus formosus	NE4		*Polyrachis* (*Campomyrma*) JDM sp. 703	PE3
	Dolichoderus glauerti	NA2		*Polyrachis* (*Campomyrma*) JDM sp. 901	KE1
	Iridomyrmex agilis gp. JDM sp. 85	NA3		*Stigmacros pilosella*	MD3
	Iridomyrmex exsanguis	KE3			
	Iridomyrmex reburrus	BB1			

Biogeographic distribution

There were a number of species that were placed in more than one biogeographic region (BR). There were 34 species that traversed both the southern and arid zones and 22 that spanned arid and tropical zones. A number of species (43) were considered widespread, i.e. found in all three BR's. The majority of species found in the study area were arid in distribution (Figure 2).

Species richness and assemblage composition

Eighty-one 'unique' species removed from the data matrix are listed in Table 4. The quadrats MR5 and ZU3 yielded the greatest number of species, with 45 in each; NE4 followed as a close second with 44 species. Overall, Nerren Nerren survey area (NE) had the highest record of species, a total of 89. 'Uniques' did not make up large proportions of most of the quadrats' total species, but KE3 and MD3 had up to 20% of their species only occurring there. The Nerren Nerren survey area had the highest number of 'uniques' out of all the survey areas, with 18% of its total species occurring only there.

The PATN analysis of the species data yielded a two-way table that grouped the species into 12 assemblages (Table 5). These assemblages were then associated with the quadrats to reveal eight quadrat groupings. These eight quadrat groups are displayed in Figure 3 as a dendrogram, showing the measure of dissimilarity between quadrat groups.

Assemblage 1 appeared to be a large mix of species, possessing no particular association with any quadrat group. All the other assemblages demonstrated some degree of clustering within one or two quadrat groups. Assemblage 2 had a majority of species falling into quadrat Group 4, which was characterised as being 'near coastal sand dunes and plains'; the assemblage was classified as mostly southern and widespread in biogeographic affinities.

Assemblage 3 had close associations with the same quadrat group, though the majority of the assemblage had an arid zone distribution and contained more tropical representatives than southern. Assemblage 3 had a weak clustering in Group 5, which was composed of only NE quadrats, two of which were in the SWBP. This variability in the NE environment is demonstrated by Assemblage 5, which has an almost equal balance of arid zone and southern species (Figure 2).

Assemblage 8 was unique within the assemblages in that it contained only two species of ant, which were present only within Group 6 quadrats. The geomorphologic characteristic of these quadrats was 'samphire bushland,' and these were the only sites in the study area with this feature. These two ants, *Cerapachys gilesi* and *Melophorus wheeleri*

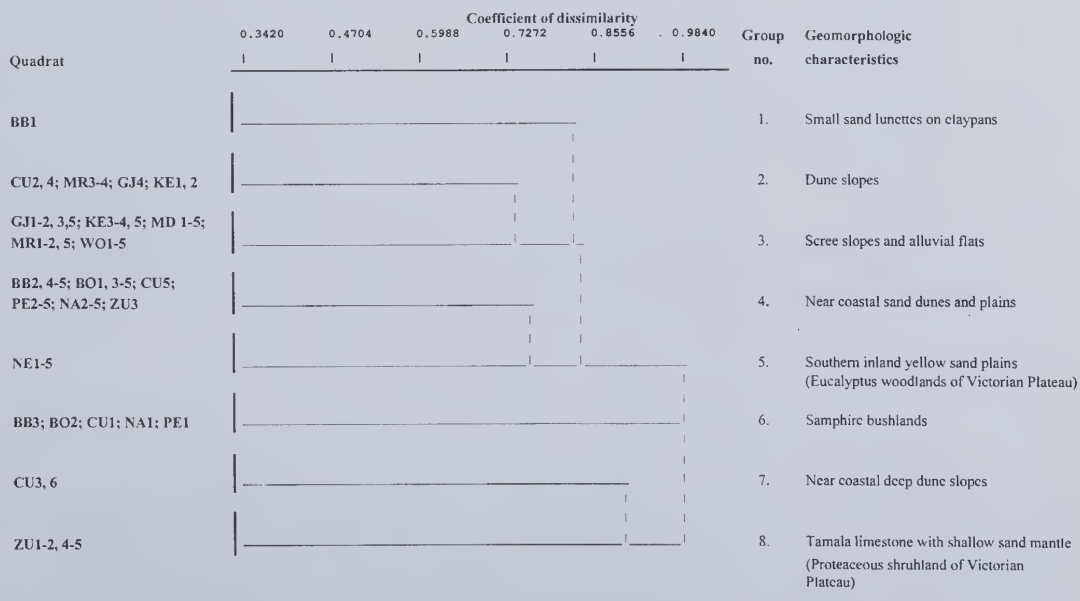


Figure 3 Dendrogram showing the groupings of quadrats according to similarity of species composition, based upon the two-way table generated by the species co-occurrence matrix (Table 4). The cut-off for the degree of dissimilarity between sites was set at 0.7272. If a dendrogram line did not meet this cut-off point, the quadrats were considered too dissimilar to be grouped together. Brief characteristics of the grouped quadrats are displayed in the final column; the location of each quadrat is shown in Figure 1

Table 5 Two-way table showing the quadrats grouped according to the 12 species assemblages. Unique species have been removed from the matrix. Each asterisk represents a species occurrence at that quadrat, the locations of which are shown in Figure 1. A dark highlighted box contains >40% of species in that assemblage; lighter highlighted boxes contain an additional 30% of species; unhighlighted boxes contain the remaining species.

Group no.	1	2	3	4	5	6	7	8
Quadrat codes / species	B B 1	CMCGMKK URUJREE 2444312	GKGGMMMMGMKMMKWWWWWW JEJJDDDDDJRERREOOOOO 13355412321525421453	BBBBBBBCPNNNNZPPP BBBOOOOUEAAAAUEEE 25415345224353345	NNNNN EEEEE 13245	BBPCN BOEUA 32111	CC UU 36	ZZZZ UUUU 1245
Assemblage 1								
Anochetus armstrongi	*		*	*		**		*
Iridomyrmex sanguineus	*		* * *	**		*		
Leptogenys clarki			***	*** * **		*****		
Odontomachus ruficeps	*		*	** * **		*** *		
Rhytidoponera violacea				* ** *	* *	* **	*	
Camponotus claripes		*	* ** *****	*	* *			
Pheidole hartmeyeri	*		*** **	* **	* *			
Melophorus bruneus complex JDM sp. 472	*		**** ** *	*** ** *	*			*
Monomorium laeve			* **** **	** *				
Leptogenys darlingtoni			** ***					
Aphaenogaster barbigula		*	*	** *** *****	* *	*		** *
Melophorus insularis		*******	* *	** ** **********	*			*
Pachycondyla lutea	*	**		******* *******	**		*	*
Solenopsis clarki	*		* * *	* * * * ****	*		*	
Iridomyrmex mattiroloi splendens		* *	* * **** **	****** * ***	*	*		****
Melophorus ANIC sp. 3		***	* ***** *	** **** * *** *	***		*	*
Pachycondyla piliventris regularis			***	* ****** *****	*****	** *		***
Melophorus JDM sp. 176	*	*** *	* * ** * *	* * **	***	**	*	*
Monomorium sordidum	*	***	* ** ** *	* **** **	* **	*		**
Pheidole nr. *variabilis* JDM sp. 177	*	** *	* * ** *	* ***** * * * **	**	*		***
Meranoplus JDM sp. 74		* *	* **	* ** * **	*			*
Camponotus oetkeri		* *		* ** * ***	* *		**	
Iridomyrmex JDM sp. 133		****	* * ***	*** **** *	** *	*		
Tetramorium nr. *striolatum*		* * *	* *	* * * * * * *	****		*	*
Camponotus gibbonotus	*	* ****	********************	*** ******** ***	*****	****		*
Iridomyrmex chasei concolor		*** *	************* *** *	** *** ** *******	****	*****		* *
Melophorus ludius sulla		** ***	* ****** ** ********	**** *********	*****	*	*	*
Iridomyrmex dromus		** **	*** **** ***** * *	******* ***** **	****	* *	*	***
Rhytidoponera micans		* ** *	***** ****** ******	********** * ***	** **	**	*	

Table 5 (cont.)

Melophorus turneri		***	********* * * * *	* **** *	*****	*	*	***
Monomorium fieldi		******	***** **** ****** *	* ** * *** *	** *	*	*	* **
Monomorium rothsteini	*	*	** ***** ******* ***	**** * ***	* *			**
Iridomyrmex mattiroloi continentis		* *	* ******** ** * * *	* **	*****	**		*
Iridomyrmex chasei	*	** **	******** **********	** ****** ***	*	*	*	*
Melophorus wheeleri complex JDM sp. 783		**	** *** ******	******** **			*	
Monomorium disetigerum	*	**** *	*********** * ** **	** ***** *		**	**	
Pheidole ?bos (JDM sp. 164)	*	** *	****** * ** *	* **** **** ** *		* *		
Melophorus turneri perthensis	*	** ***	* ****** *	* * ** * **				*
Polyrachis schwiedlandi complex JDM sp. 1010		* ****	* ** ****** ***	* *** *	*			
Rhytidoponera tyloxys		***	*** * ** ***	* * * **	***			* *
Monomorium sydneyense		* *	* * ** *	* * * * **	**			
Melophorus nr. *aeneovirens* JDM sp. 545		* *	* ***	**** * *	*			
Tetramorium impressum			* * * *	** ** * *		**		
Tapinoma JDM sp. 981		**	* ** * *	*** *		**		
Melophorus JDM sp. 1102		**	* * *	* * *	**	*		**
Stigmacros spinosa		**	* *	* * *	* *			
Camponotus wiederkehri gp. JDM sp. 924	*	* ****	* * ***** ***	** ***	*			
Melophorus bagoti		** ****	* ***** * * *	****				
Rhytidoponera crassinoda	*	** ****	** ** ** *	*		**		
Opisthopsis haddoni rufoniger		* * *	* ** * *	* *				
Iridomyrmex hartmeyeri gp. JDM sp. 327		**** **	** * * **	*** **				
Pheidole deserticola		* ***	* ** *	* * *		*		
Iridomyrmex rufoniger suchieri		* **	*		*			
Rhytidoponera taurus	*	* ***	***	*				
Assemblage 2								
Camponotus claripes gp. JDM sp. 229			*	* * * * *				***
Iridomyrmex bicknelli			** * *	* ** *				***
Camponotus scratius		*		* * **** * *			*	***
Cerapachys brevis		*		** ** * *				*
Crematogaster frivola				* **** *		*	*	**
Iridomyrmex JDM sp. 846				* * *** *			*	*
Melophorus JDM sp. 500	*	*		*	*			***
Rhytidoponera metallica			*	**	* *		*	****
Meranoplus JDM sp. 424			*	*	*			**
Assemblage 3								
Camponotus lownei		*	*	* *	** *			
Iridomyrmex bicknelli brunneus		*	*	* * **	*			
Rhytidoponera metallica gp. JDM sp. 1098				* ***	* *			

Table 5 (cont.)

Cerapachys fervidus			*	* ** *		*		
Iridomyrmex discors		*		* *	*			
Melophorus bruneus		*	* *	* * * *	*			
Assemblage 4								
Calomyrmex ANIC sp. 1			* ****		* **			
Crematogaster queenslandica gp. JDM sp. 1100		*	***	* * *	***			
Iridomyrmex agilis			* ** ** ***		*	**		
Camponotus discors		*	** ****** *					
Iridomyrmex hartmeyeri			** * * * *	*				
Meranoplus JDM sp. 679		*	* ***					
Polyrachis macropa	*		* ** ** **	*				
Iridomyrmex viridianeus			* *					
Tetramorium spininode		*	** *					
tramorium viehmeyeri		*	**	*				
Melophorus JDM sp. 699			* *					
Camponotus tasmani			* *	*				
Solenopsis belisarius			*	*		*		
Cerapachys greavesi			* * *	*		*		*
Tapinoma JDM sp. 78			*	*** * *	*	*		*
Colobostruma cerornata		*	*					*
Stigmacros JDM sp. 1067	*		*					*
Iridomyrmex cephaloinclinus			* *					
Iridomyrmex lividus			*			*		
Iridomyrmex JDM sp. 1028			**					
Pheidole JDM sp. 558			**					
Polyrachis (Campomyrma) JDM sp. 670		*	* *					
Assemblage 5								
Camponotus clarior				*	*			
Myrmecia ?varians				*	*			
Iridomyrmex JDM sp. 130		*	*		*			
Camponotus nigroaeneus gp nr JDM sp. 108					* *			
Camponotus prosseri		*			** *			
Assemblage 6								
Camponotus tricoloratus		*	*	* *	* *			
Melophorus JDM sp. 199			* *** *	**	*****			
Melophorus JDM sp. 784			* *	* *	* *			
Tetramorium JDM sp. 515			*	**	*			
Iridomyrmex mattiroloi complex JDM sp. 449			* *	*		*		
Rhytidoponera foveolata			* *** *	*				

Table 5 (cont.)

Melophorus mjobergi			* *	* *				*
Iridomyrmex greensladei			* *	*	* *	*		
Meranoplus JDM sp. 1101			* *		* *			
Stigmacros termitoxena			* *	*	* * *			
Monomorium leae	*		*		*			
Stigmacros JDM sp. 188			*		*			
Tetramorium JDM sp. 1007			*		* *			
Assemblage 7								
Camponotus cf. *discors* complex JDM sp. 1104			*	*				
Camponotus lownei complex JDM sp. 761		*		*				
Camponotus lownei complex JDM sp. 772				* *				
Paratrechina minutula				* * *	*			
Melophorus JDM sp. 1063			*	* * * *	*			
Myrmecia desertorum	*			* * * * *				
Monomorium eremophilum			* *	* * *				
Tetramorium JDM sp. 461			*	* * *		*		
Cerapachys brevicollis			*	*				
Melophorus bruneus complex JDM sp. 951				*		*		
Crematogaster queenslandica gp. JDM sp. 1099		*		* *			*	
Stigmacros JDM sp. 341			*	*				
Crematogaster JDM sp. 859			*	*				
Monomorium striatifrons			*	*				
Assemblage 8								
Cerapachys gilesi						* *		
Melophorus wheeleri complex JDM sp. 1077						* * * *		
Assemblage 9								
Cerapachys incontentus	*			*				
Iridomyrmex JDM sp. 597	*			*				
Polyrachis gravis	*	*		* *				
Polyrachis sidnica complex JDM sp. 390			*	* *				
Tetramorium JDM sp. 884				* *				
Assemblage 10								
Calomyrmex glauerti		*	* * * *					*
Cerapachys sjostedti		* * *	*					*
Cerapachys clarki		*		*				*
Polyrachis cf. *sidnica* complex JDM sp. 671		*		*				* *
Doleromyrma darwiniana	*	* *		*		*		
Monomorium nanum	*	*	* *	*		*		
Iridomyrmex JDM sp. 319		*	* * *					

Table 5 (cont.)

Melophorus wheeleri		*	* *			*		
Dolichoderus JDM sp. 838		*			*			
Polyrachis (*Campomyrma*) JDM sp. 805		*			*			
Iridomyrmex bicknelli azureus		**						
Myrmecia callima		**						
Tetramorium sjostedti		**						
Notoncus capitatus		* *						
Assemblage 11								
Camponotus cinereus				* *	*			
Crematogaster dispar		*		* *	*			
Monomorium rufonigrum	*		*	*		*		
Monomorium legulus				*	*			
Ochtellus JDM sp. 851				**				
Assemblage 12								
Camponotus claripes minimus				** *				*
Melophorus ?JDM sp. 470			*	*				*
Plagiolepis squamulosa					*			**
Camponotus claripes gp. JDM sp. 63								* *
Camponotus rufus								****
Paratrechina minutula gp JDM sp. 916				*				*
Stigmacros aemula			*	*				*
Camponotus terebrans				* *				**
Crematogaster queenslandica gp. JDM sp. 428				*	*			***
Notoncus gilberti				*	*			**
Stigmacros reticulata				* **				**

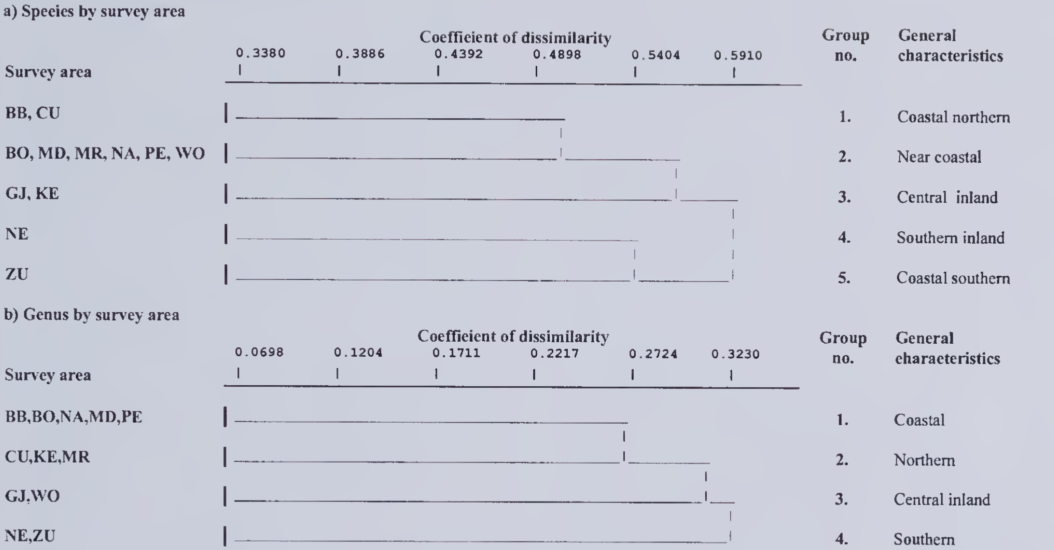


Figure 4 Dendrograms showing the groupings of survey areas according to similarity of a) species composition and b) genus composition, based upon two-way tables generated by the species/genus co-occurrence matrix for each survey area. Brief generalisations of the grouped survey areas are displayed in the final column.

complex JDM sp.1077 are very different in that the former is a common ant around the Perth hinterland and the latter is more common in the drier arid zone regions to the north.

Both species have been recorded for the SWBP, but presumably it is the first time that both species have been associated together in the saline areas of samphire bushland. No other assemblage was associated with this group of quadrats.

Figure 4a provides an analysis of the species in terms of survey areas, instead of individual quadrats. This revealed five groupings of survey areas on the basis of species. These survey area groups (numbered clouds) are displayed in Figure 5a, which reveals a separation of north and south faunas (clouds 1 and 3: 4 and 5), as well as inland and coastal assemblages (clouds 1: 3 and 4: 5). This pattern was further simplified in Figure 4b, where ant genera analysed against the survey areas revealed a slightly different association of survey areas. The survey area groups in Figure 5b further emphasize a more north-south separation (clouds 2: 4).

Environmental variables

The environmental parameters revealed some correlations with the patterns of distribution in terms of species, as well as with genera. Regarding the 12 species assemblages, almost all environmental variables were significantly associated ($P > 0.05$) except for stoniness, over-bank stream flow and soil exchangeable sodium. The environmental variables associated with the survey area groups revealed some clearer patterns. There appeared to be a pattern relating species distribution to maximum temperature, precipitation

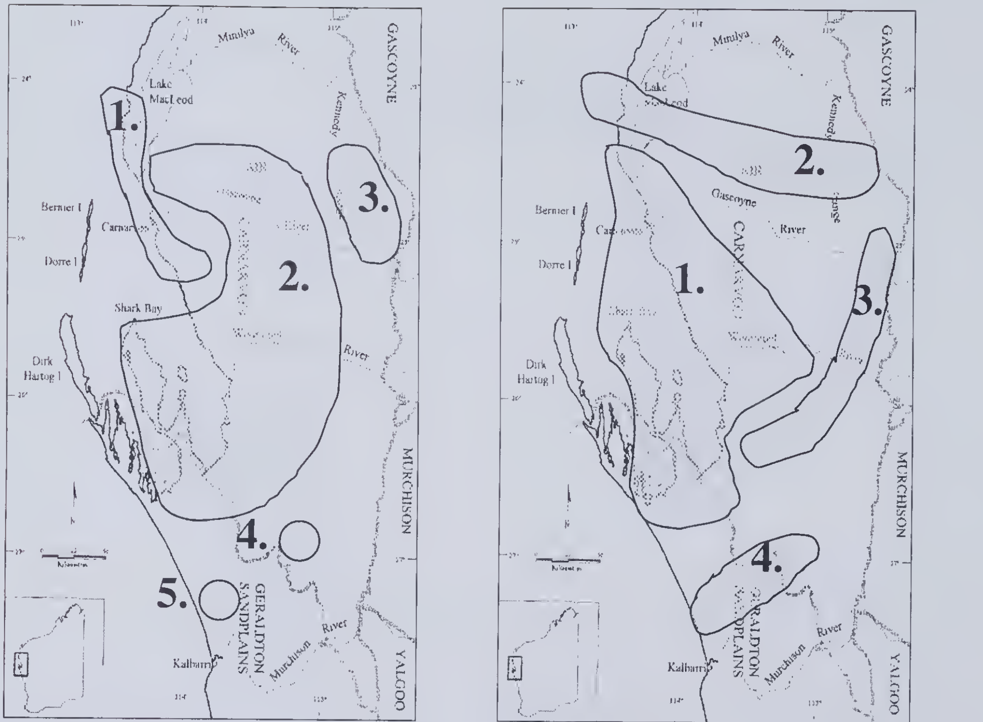
Table 6 The climatic and geographical variables associated with the 5 survey area groups generated by the species assemblages and 4 survey area groups generated by the genera assemblages. Only significant values ($P < 0.05$) revealed by a Kruskal-Wallis Test are given.

a) Species by survey area

Environmental variable	P
Maximum warmest period temperature	.048
Temperature annual range	.056
Warmest quarter temperature	.029
Annual average precipitation	.025
Wettest quarter precipitation	.049
Coldest quarter precipitation	.033
Altitude	.006
Longitude	.050
Coastal Distance	.023

b) Genus by survey area

Environmental variable	P
Annual average temperature	.009
Warmest quarter temperature	.046
Coldest quarter temperature	.034
Annual average precipitation	.050
Warmest quarter precipitation	.037
Coldest quarter precipitation	.043
Latitude	.009



a) Species assemblage b) Genus assemblage

Figure 5 The southern Carnarvon Basin study area. Each shaded cloud shows the groupings of survey areas exhibiting similarities in terms of a) species assemblage and b) genus assemblage. The numbers on the clouds correspond to the survey area groups displayed in Figures 4a and b.

during the wet season, altitude, longitude and coastal distance. This was reflected somewhat in the genus assemblages, showing an association with temperature, precipitation and latitude (Table 6).

These associations with environmental variables for survey areas reflect the patterns seen in Figures 5a and b. The differences between species assemblages and genus assemblages are characterised by the fact that the species assemblages are separated by altitude, longitude and coastal distance, while genus assemblages were separated by latitude. Figure 5a shows a separation from coastal areas to inland, and from lowland to highland, whereas Figure 5b demonstrates a separation from north to south, with less of a coastal to inland separation.

DISCUSSION

Biogeography

The ants of the southern Carnarvon Basin are highly species rich, although some of the 243 species could not confidently be placed in any one biogeographic region; overall there was a greater tendency for species to have an arid zone distribution than a southern one, and much less a tropical or widespread distribution. The overlap between arid zone and southern elements of this study demonstrates the transitional nature of this area.

A majority of the ant species are represented in the SWBP, with a number of them being present at the limit of their ranges in the southern two survey areas, ZU and NE. Gibson *et al.* (2000) suggest that the phytogeographic boundary established by Beard should be located more to the south and to the west in order to exclude some of the arid vegetation types found around Shark Bay. This is supported by the fact that the NA survey area (technically located in the SWBP) was grouped with the more northern survey areas, in contrast with ZU. The species assemblage at NE also contains fauna that are considered more arid zone, suggesting that both these sites should not be included in the SWBP. If the SWBP boundaries were moved more southerly and westerly, this would better account for the species occurrence at these two sites.

Nerren Nerren was unusual in that its quadrats spanned the phytogeographic boundary between the south-west and arid regions. It contained a high

number of uniques, which corresponds with the fact that NE2 fell into its own individual vegetation grouping, that also appeared to be a transitional area. This site may be of great ecological importance in terms of investigating flora and fauna that have adapted to the variable nature of the area.

Patterns of association related to environmental variables

Climate appears to play a prominent role in the distribution of the ant species. Both the quadrat and survey area analyses showed significant associations with temperature and rainfall. Although the quadrat analyses demonstrated significance for all climatic variables, the survey area data were able to give more specific associations such as with temperature. Ants have been positively correlated with temperature in other studies (Briese and Macauley 1981, Vanderwoude *et al.* 1997), which demonstrates their relation to vegetation and to soils; both these factors would heavily influence ant species distribution (Greenslade and Thompson 1981, Morton 1982, Andersen 1993).

While Gibson *et al.* (2000) found that the vegetation boundaries were highly correlated with edaphic factors, (supporting their suggestion to move the phytogeographical boundary) the ant species assemblages did not seem to focus on any particular soil factor. Lobry De Bruyn (1999) suggests that ants are good soil quality indicators in natural and rural environments. Although the results from this current study support this idea, the broad base and wide range of the research area may have clouded any particular soil factor associations that could be derived from the ant species distribution.

Rainfall was also positively associated with the ant species assemblages. There is an increasing amount of variability in mean precipitation moving northwards in the study area, due to irregularity of summer monsoonal rainfall. This trend is reversed in the more southern areas, which are subject to regular winter rains. The separation of southern and northern faunas reflects these precipitation differences, which may be further enhanced by the coastal – inland differences in rainfall volume. Rainfall, or lack of, can influence ant species distribution to a great degree. For example, it results in a more *Iridomyrmex* – dominated landscape in the arid areas and more cryptic species in wetter areas (Greenslade 1985). While species abundance was not measured, the current study demonstrates a more *Camponotus* / *Melophorus* – dominated landscape.

The nature of the species composition observed in this study supported the two major groups of ant genera established by Greenslade and Greenslade (1989). Based on broad ecological and geographical trends, they separated the 'core' groups of ants (Group I: *Iridomyrmex*, *Melophorus* and *Camponotus*) from the other more specialised genera (Group II) such as *Monomorium*, *Pheidole* and *Rhytidoponera*. Using data derived from different eastern states' studies, they hypothesized that high competition from Group I species would reduce species diversity of Group II species, but in situations where the ratio of Groups I/II is low, the high diversity may be due to areas being in transition zones where Group I taxa are outside their climatic optima. This theory is supported by results of this study, as it shows that there is a relatively low ratio between the Group I species (103 spp.) and Group II species (89 spp.).

Wyrwoll *et al.* (2000a) also found that there was a more pronounced north – south gradient for mean coldest quarter temperature, which is in concordance with the genus assemblages generated for the survey areas. Table 6b shows that there is a significant association between genus assemblages and coldest quarter temperature; Figure 5b further demonstrates this, showing that the assemblages display a more north – south separation of survey area groups. Recent studies have found that species richness in ants can be related to latitudinal gradients, even at small scales (Gotelli and Ellison 2002). Though the current study site spanned roughly only four latitudinal degrees, latitude was significantly associated with the genus assemblages (Table 6b). While species assemblages did not have a significant association with latitude, perhaps a further study of species richness may generate a relationship. It would be of interest to see whether genus to species ratios can be made more predictive over smaller latitudinal gradations.

Overall, there is a difference between species and genus assemblages; the former closely follows vegetational patterns, while the latter tends towards latitudinal gradients. Genus richness has been found to be an inadequate indicator of species richness, as there is a high amount of variability in species to genus ratio, depending on the region (Andersen 1995). While the southern sites NE and ZU displayed a relatively lower ratio (i.e. similar numbers of species and genera) than the northern survey areas, NE separated out again in that it had a ratio more similar to the northern survey areas. This discrepancy also cropped up in the CU and BO survey areas, which also showed very low ratios. In this case, it appears that the species to genus ratio follows the trend found in southern semi-arid zones and northern semi-arid zones, where the mixing of genera (cool temperate genera from the south and tropical genera from the north) causes a lower ratio (Andersen, 1995). This lends further support to the fact that this area is a major transitional zone, which therefore should be taken into consideration as a biogeographically and ecologically significant area.

The general ant species distribution appears to follow the modified phytogeographic zones suggested by Gibson *et al.* (2000), but further studies on individual species would be required in order to establish ranges and provide a concrete basis for determining biogeographic origin. This study contributes to a growing pool of data that can be used to compile a complete bio-inventory of all ant species for Western Australia.

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Distribution of the family Littorinidae (Mollusca: Gastropoda) in Thailand

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Abstract – The distribution of the family Littorinidae in mangroves and on rocky shores in Thailand was studied. Fourteen species of *Littoraria, Echinolittorina* and *Peasiella* were recorded from 50 survey sites, bringing the total known for the country to 16 species. Two species were recorded for the first time in Thailand. *Littoraria conica* was found in only two places in southern Thailand, both on the Andaman Sea. *Echinolittorina feejeensis* occurred on scattered granite rocks on sandy beaches in the splash zone of offshore islands where the water is clear both in the Gulf of Thailand and the Andaman Sea. It is dominant at Ko Kumpun, Trat Province. Habitats occupied by the three genera are distinct. *Echinolittorina* and *Peasiella* occur primarily on intertidal rocks though occasional individuals are found in the seaward fringe of mangroves; *Littoraria undulata* occupies a similar rock habitat. The other species of *Littoraria* occur on many species of mangroves, with some occasionally being found on rocks. Four species (*L. bengalensis, L. conica, L. scabra,* and *L. undulata*) occurred only on the Andaman Sea side of Thailand. *Littoraria bengalensis* is restricted to the Indian Ocean but the other three species occur in the Pacific Ocean east of Thailand. Their absence in the Gulf of Thailand appears to be real.

INTRODUCTION

The family Littorinidae is a moderately diverse group of intertidal gastropods. Reid (1989a) reported there were 173 species, and more species have since been described. The family is most diverse in the Indo-West Pacific Ocean. Rosewater (1970, 1972) examined the distribution of the family in the entire Indo-Pacific using records from the major museum collections. He considered there to be one subspecies of the mangrove littorine, *Littorina scabra,* a view reiterated in a subsequent paper (Rosewater, 1980). Reid (1986a) was able to examine the species in a wide range of field localities and determined there was a suite of 20 species inhabiting different parts of the mangroves and rocky shores. He transferred the group to the genus *Littoraria.* He later (Reid, 1999) extended the study of *Littoraria* into the eastern Pacific. Reid subsequently expanded his research into several other genera of tropical Indo-Pacific littorinids, including *Mainwaringia* (Reid, 1986b), *Peasiella* (Reid, 1989b; Reid and Mak, 1998), *Nodilittorina* (Reid, 2001a), and a paper on the littorinids of Hong Kong (Reid, 1992). Williams *et al.* (2003) transferred the tropical Indo-Pacific *Nodilittorina* species to *Echinolittorina.* Reid also recorded three species of Indo-West Pacific littorines in the eastern Pacific (Reid and Kaiser, 2001). Despite their intertidal nature and the tendency for a widespread distribution, new species of Indo-Pacific littorines continue to be found, including species of *Littoraria* (Reid, 2001b; Stuckey and Reid, 2002) and *Tectarius* (Reid and Geller, 1997). Many of the papers cited above have recorded species of littorinids in Thailand as part of broad distributional studies, but the Littorinidae of Thailand have not been examined in detail. Altogether, 14 species of littorinids have been recorded, including nine *Littoraria,* three *Echinolittorina* and two *Peasiella.* McQuaid (1996a; 1996b) presented a general review of the biology of littorinids.

Molluscs are an important component of the fauna of mangrove communities in the tropical and subtropical Indo-West Pacific, including Thailand. They are diverse (Macnae, 1967, 1968; Saenger *et al.*, 1977), and many species have a high density and/or biomass (Brown, 1971; Wells, 1983, 1984, 1986). Species living in mangroves can be divided into those that are found on adjacent rocky, sandy and muddy shores, and which simply use mangroves as an incidental habitat, and species that are restricted to mangroves. Cantera *et al.* (1983) concluded that only 20% of the gastropods in mangroves are species restricted to the tree zones. These characteristic mangrove species are often numerically dominant and ecologically important. Many have developed mechanisms such as resorbing calcium carbonate from internal shell

structures which allow them to survive in this difficult habitat (Vermeij, 1974, 1978). While there are numerous species of molluscs living in mangroves, there is very little information on their lifespan or population dynamics. *Littoraria* is particularly interesting as a mangrove mollusc genus, as most of the species occur only in mangroves, where they are the dominant molluscs in the trees, while most other mangrove gastropods live on the ground.

Most of the records of littorinids in Thailand are based on museum material collected over many years, but there have been several studies which examined distribution and/or biology of the group. Frith *et al.* (1976) studied zonation of macrofauna on a mangrove shore at Phuket Island. Details of the littorinids collected in this study were reported in a short paper by Nielsen (1976). As part of a broader study of habitat and zonation patterns of *Littoraria* in the Indo-West Pacific, Reid (1985) included sites at Phuket Island and Kanchanadit. Cook and Garbett (1989) detailed patterns of variation in mangrove littorinids at Phuket Island.

The records of littorinids in Thailand are generally patchy, with only a few localities recorded for a country with extensive coastlines on the Pacific Ocean (Gulf of Thailand) and in the eastern Indian Ocean. The present paper is the first detailed examination of littorinids in Thailand as a basis for understanding where the species occur in Thailand to facilitate future work on their biology.

MATERIALS AND METHODS

Snails used in this study were collected from November 2001 to August 2003 from all coastal parts of Thailand, including the eastern provinces (Chonburi, Rayong, Chanthaburi and Trat), the middle provinces (Samut Prakan and Samut Songkram), the east coast of the southern provinces (Phetchaburi, Prachuab Khiri Khun, Chumphon, Surat Thani, Nakhon Si Thammarat, Pattani, and Narathiwat) and the west coast of the southern provinces (Ranong, Phang Nga, Phuket, Krabi, Trang, and Satun).

Adult specimens of similar sizes were collected by hand in two habitats. Specimens were collected from roots, trunks and leaves in mangrove areas and some animals were collected from nearby mud. Other species were collected in the splash zone of rocky shores along the islands. One to three habitats were examined at each locality. After collection, all specimens were narcotised in a 7.5% (weight/volume) solution of magnesium chloride (Reid, 2000, 2001b) then fixed in 10% formalin and retained for later dissection and identification. Representative material of all species is retained in the mollusc collections of the Burapha Institute of Marine Science, Burapha University.

Rosewater (1970, 1972) and Reid (1986a and other papers) described the shells and anatomy of these species. As they can usually be identified from shells alone, the details are not repeated here. As Reid (1986a) is not widely available in Thailand, shell photographs of all species collected are presented in Figures 1 and 2. *Littoraria strigata* and *L. articulata* are unusual in that they cannot be differentiated by their shells. Males are readily determined using the structure of the penis (Figure 2). As the differentiation of females is subtle, all records in this paper are based on males. The dendrogram was calculated using the Statistical Package in the Social Sciences (SPSS), Version 11.0.

RESULTS

Fourteen species: 10 *Littoraria*, 3 *Echinolittorina* and 1 *Peasiella* were recorded from 50 survey sites (Figure 3, Appendix 1, Table 1). The number of stations at which each species was found ranged considerably, from 32 for *L. strigata* to 2 for *L. conica*. Aside from *L. strigata*, the other widespread species were *E. trochoides* (26 stations), *L. articulata* (19), *E. vidua* (17), *L. pallescens* (17), *L. melanostoma* (16), and *L. carinifera* (14). The 10 species of *Littoraria* occurred at a mean of 11.5 ± 9.8 (SE) stations, the three *Echinolittorina* at a mean of 16.7 ± 5.5, and the single *Peasiella* at seven stations. It was interesting that the two species which are indistinguishable on the basis of shell morphology, *L. articulata* and *L. strigata* co-occurred at all 19 of the stations at which *L. articulata* was found. In addition, *L. strigata* was found at 13 stations where *L. articulata* did not occur.

Habitats occupied by the three genera are distinct. Nine of the 10 species of *Littoraria* occur primarily on mangroves (Table 1). They tend to occur on a wide range of mangrove and other plant species in the community. In all *Littoraria* were recorded from a total of 17 species of plants. The mean number of plant species inhabited by the mangrove *Littoraria* was 9.2 ± 1.2. The common species occurred on a wide range of plants: *L. carinifera* was found on 14 species, *L. melanostoma* and *L. pallescens* on 13, and *L. articulata* on 11. Many of these species also were found on house or pier poles, which were often of wood. Several were also found on rocky shores, but this constituted only a small portion of the population. It was noteworthy that four species (*L. articulata, L. carinifera melanostoma* and *L. strigata*) were found on mud or sand among the mangroves. This was a natural occurrence, and not simply that the animals were inadvertently brushed off the trees by the investigator. *Littoraria* collected in this study were most abundant near the seaward margins of the mangroves; density declined sharply with distance from the edge of the mangroves. Aside from *L. pallescens*, most individuals were found <50 cm

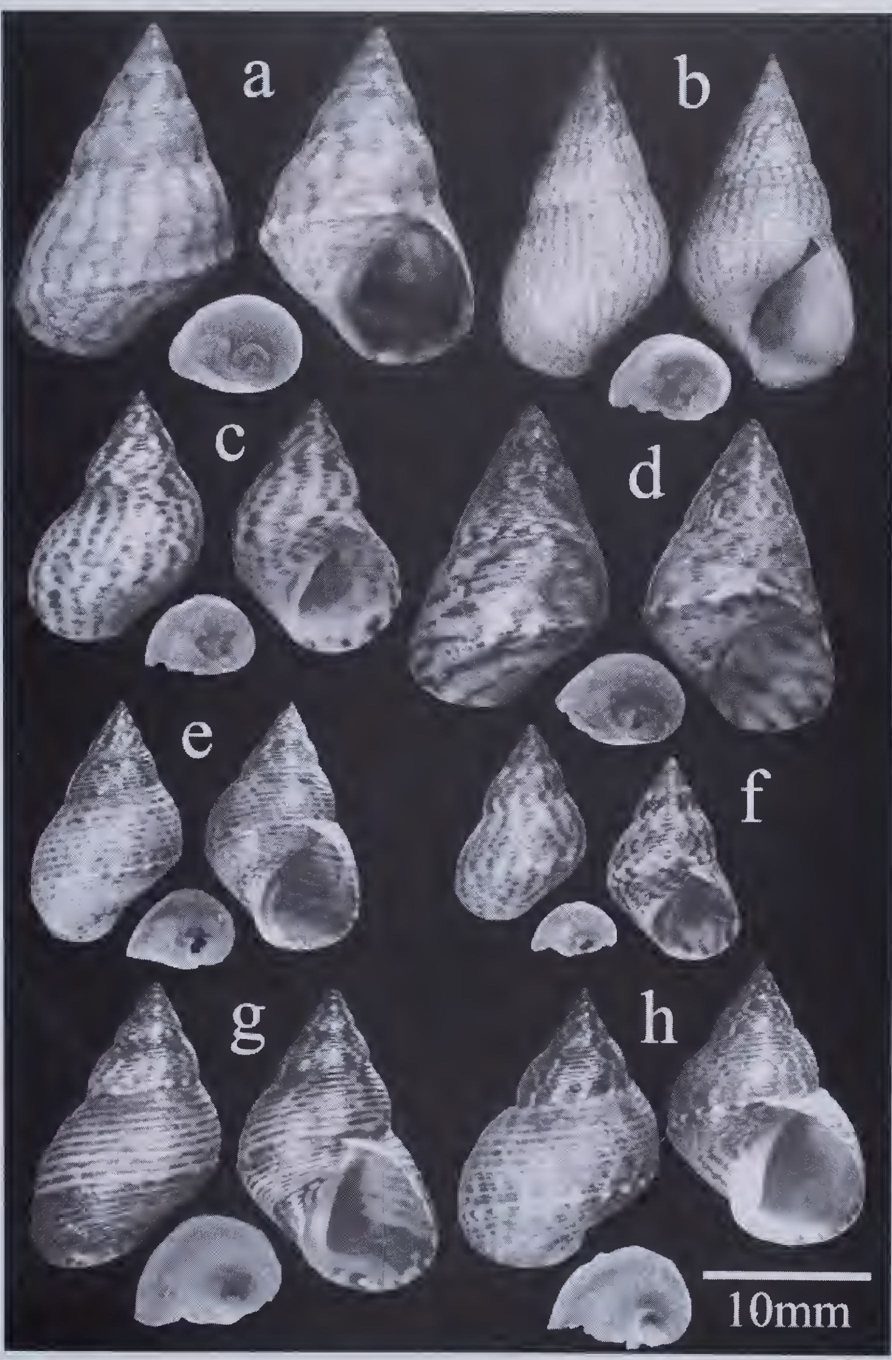

Figure 1 Littorinids recorded from Thailand. a. *L. carinifera*, Ban Jebilung, Amphur Moeng, Satun Province (BIMS-M1175) b. *L. melanostoma*, E-led canal, Chumphon Islands Marine Park, Tumbon Hadsairee, Amphur Moeng, Chumphon Province (BIMS-M1176) c. *L. articulata*, Samed, Amphur Moeng, Chonburi Province (BIMS-M1177) d. *L. conica*, Ban Jebilung, Amphur Moeng, Satun Province (BIMS-M1178) e. *L. bengalensis*, Chaomai Beach, Tumbon Ko Libong, Amphur Kuntung, Trang Province (BIMS-M1179) f. *L. intermedia*, Mai ngarm Bay, Ko North Surin, Phangnga Province (BIMS-M1180) g. *L. pallescens*, Ban Dee, Tumbon LaemPo, Amphur Yaring, Pattani Province (BIMS-M1181) h. *L. scabra*, Mai ngarm Bay, Ko North Surin, Phangnga Province (BIMS-M1182)

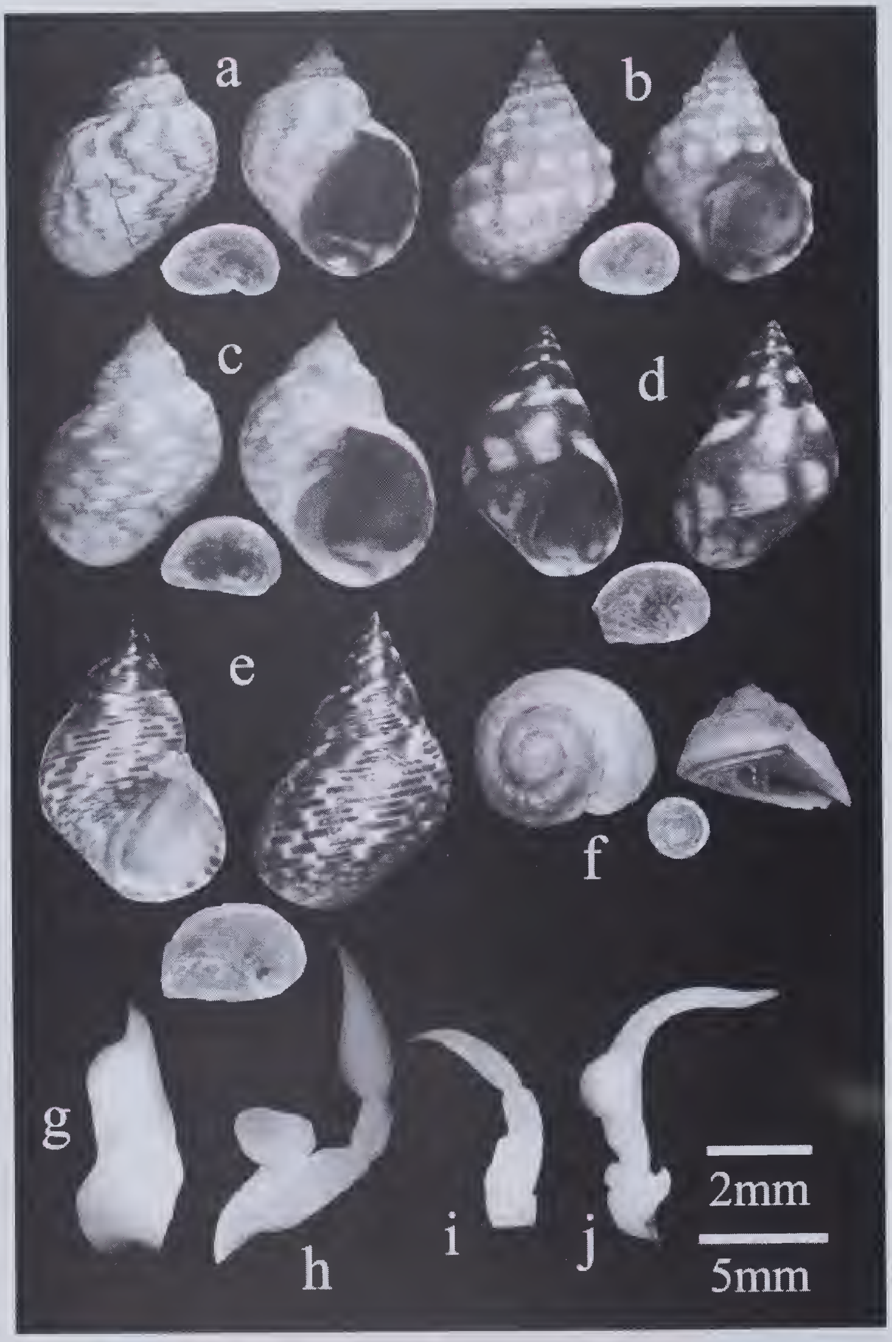

Figure 2 Littorinids recorded from Thailand. a. *E. feejeensis*, Ko Kumpun.(BIMS-M1185) b. *E. trochoides*, Ko Prao-nok, Sub-amphur Ko Chang.(BIMS-M1186) c. *E. vidua*, Yai Bay, Sub-amphur Ko Kut, Trat Province.(BIMS-M1187) d. *L. undulata*, Had Kalim, Amphur Kratu, Phuket Province.(BIMS-M1183) e. *L. strigata*, Ban Cha-ngoe, Tumbon Takienthong, Amphur Kanjanadit, Surat Thani Province.(BIMS-M1184) f. *P. roepstorffiana*, Mai ngarm Bay, Ko North Surin, Phangnga Province.(BIMS-M1188) g. Penis of *L. articulata*, Samed, Amphur Moeng, Chonburi Province. h. Penis of *L. bengalensis*, Chaomai Beach, Tumbon Ko Libong, Amphur Kuntung, Trang Province. i. Penis of *L. intermedia*, Mai ngarm Bay, Ko North Surin, Phangnga Province. j. Penis of *L. strigata*, Ban Cha-ngoe, Tumbon Takienthong, Amphur Kanjanadit, Surat Thani Province. Scales for a – e = 5mm; f – j = 2mm.

Table 1 Habitats occupied by littorinids in Thailand.

Species	No. stations	Habitats occupied
Littoraria articulata (Philippi, 1846)	19	Rocks and seawalls, house and pier poles, muddy sand, mangroves: *Rhizophora mucronata, Rhizophora apiculata, Avicennia alba, Avicennia marina, Sonneratia alba, Sonneratia griffithii, Sonneratia caseolaris, Lumnitzera racemosa, Ceriops decandra, Ceriops tagal.* Sedge: *Sesuvium portulacastrum*
Littoraria bengalensis Reid, 2001	6	Mangroves: *A. alba, A. marina, S. griffithii, R. apiculata, C. decandra, Aegialites rotundifolia.* Ground cover: *Finlaysonia maritima.*
Littoraria carinifera (Menke, 1830)	14	Rocks and seawalls, house and pier poles, muddy sand, mangroves: *R. apiculata, R. mucronata, A. alba, A. marina, C. tagal, Bruguiera cylindrica, Xylocarpus granatum, S. griffithii, L. racemosa, C. decandra, A. rotundifolia. Nypa fruticans.* Climber: *F. maritima.* Sedge: *S. portulacastrum.*
Littoraria conica (Philippi, 1846)	2	Mangroves: *R. apiculata, R. mucronata, C. decandra* and *A. rotundifolia* Climber: *F. maritima*
Littoraria intermedia (Philippi, 1846)	3	Rocks and seawalls, mangroves: *R. apiculata, A. alba, A. marina* and *S. griffithii*
Littoraria melanostoma (Gray, 1839)	16	Rocks and seawalls, muddy sand, mangroves: *A. marina, A. alba, R. apiculata, R. mucronata, S. griffithii, S. caseolaris, S. alba, C. decandra, A. rotundifolia, L. racemosa, C. tagal.* Sedge: *S. portulacastrum.* Climber: *F. maritima,*
Littoraria pallescens (Philippi,1846)	17	Rocks and seawalls, house and pier poles, mangroves: *R. apiculata, R. mucronata, A. alba, A. marina, S. griffithii, S. alba, L. racemosa, C. decandra, C. tagal, B. cylindrical, X. granatum* and *A. rotundifolia* Palm: *Nypa fruticans.*
Littoraria scabra (Linnaeus, 1758)	3	Rocks and seawalls, mangroves: *R. mucronata, R. apiculata, A. alba, A. marina* and *S. griffithii*
Littoraria strigata (Philippi, 1846)	32	Rocks and seawalls, house and pier poles, muddy sand, mangroves: *R. mucronata, R. apiculata, A. alba, A. marina, S. alba, S. griffithii, S. caseolaris, L. racemosa, C. decandra, C. tagal.* Sedge: *S. portulacastrum*
Rocky shore species		
Littoraria undulata (Gray, 1839)	3	Rocks and seawalls
Echinolittorina feejeensis (Reeve, 1857)	7	Rocks and seawalls
Echinolittorina trochoides (Gray, 1839)	26	Rocks and seawalls, mangroves: *R. apiculata* and *A. marina*
Echinolittorina vidua (Gould, 1859)	17	Rocks and seawalls, mangroves: *A. marina*
Peasiella roepstorffiana (Nevill, 1885)	7	Rocks and seawalls

from the sediment, and few were above 1 m. On the lower parts of the trees they occurred widely on trunks, pneumatophores, branches, and leaves. *Littoraria pallescens* occurred primarily in the foliage higher up on the trees at heights of up to 5 m. *Echinolittorina* and *Peasiella* occur on primarily on intertidal rocks though occasional individuals were found in the seaward fringe of mangroves; *Littoraria undulata* occupied a similar rock habitat.

A dendrogram calculated on the occurrences of all species at all 50 stations (Figure 4) demonstrates that there are two clear assemblages: seven species of *Littoraria* which live in close association with mangroves, and seven species which tend to occur on rocky shores, though they also occur in mangroves. The latter group includes the rocky shore *L. undulata* and two mangrove species, *L. intermedia* and *L. scabra.*

DISCUSSION

Rosewater (1970, 1972) and Reid (1986a, 1989b, 2001a, 2001b; Reid and Mak, 1998) reported 14 species of littorinids in three genera in Thailand as part of their broader surveys of Indo-Pacific Littorinidae. All except two of these species were reported in the present paper, with many additional localities presented for most species. Reid (2001) found *Echinolittorina reticulata* along the western coast of Thailand but it was not found in the present study. *Peasiella patula* was recently described from Singapore by Reid and Mak (1998), with a record of Pattaya, Thailand included in the description. A trip was made to Pattaya and the nearby islands to search for this species, but the record could not be confirmed. Two species were recorded for the first time in Thailand. *Littoraria conica* was found in only two places in southern Thailand, both on the

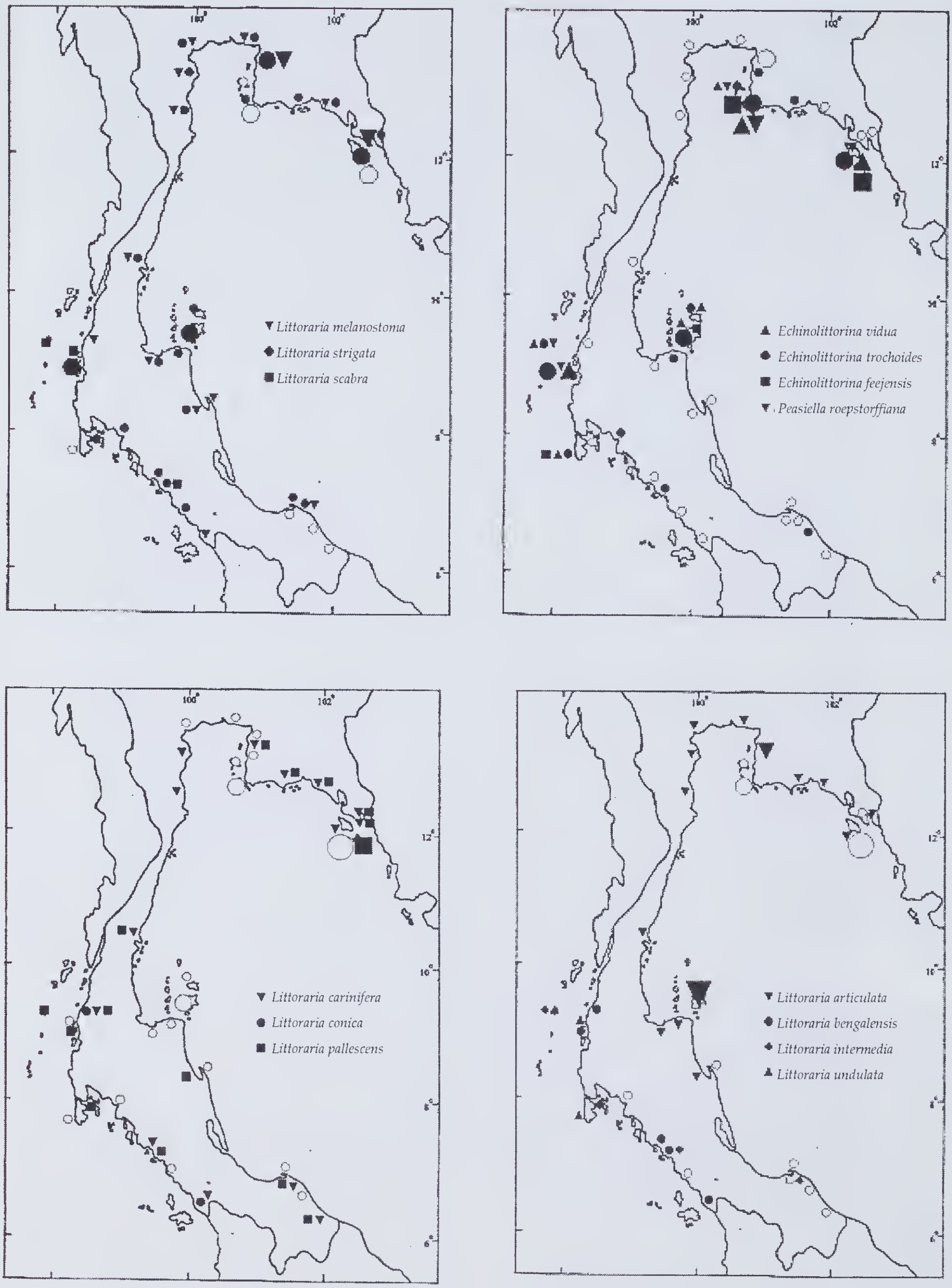

Figure 3 Distribution maps of littorinids in Thailand. Empty circles represent stations at which none of the mapped species were found. Larger symbols indicate records from more than one station that are too close to separate on the map.

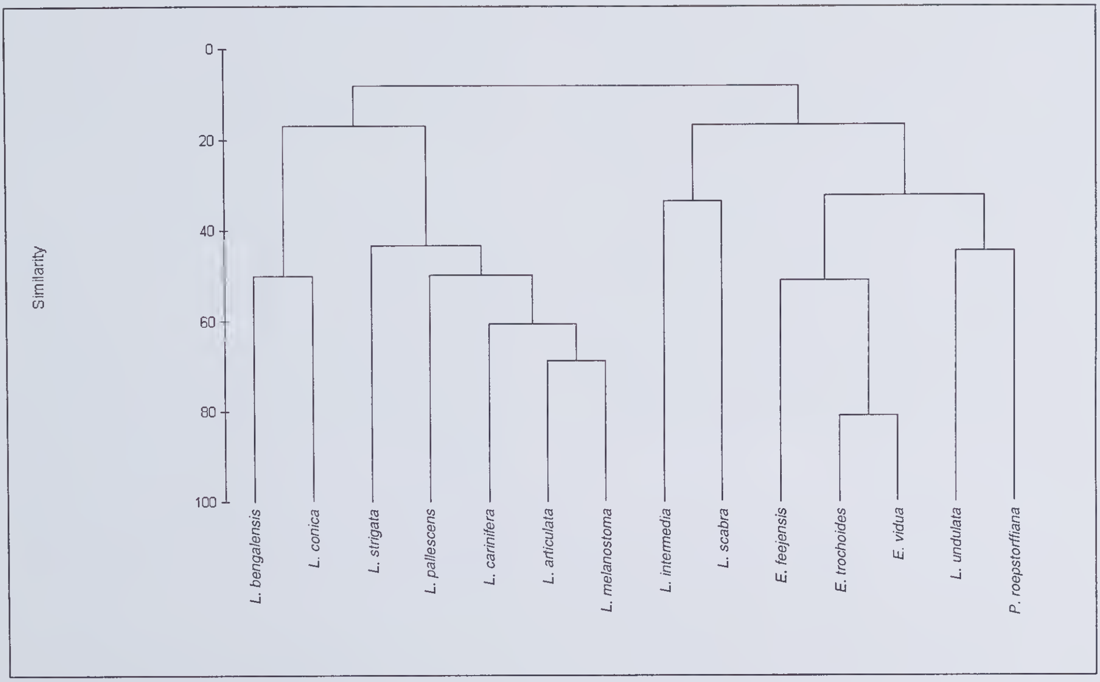

Figure 4 Dendrogram of similarity of littorinids collected at 50 stations in Thailand.

Andaman Sea. *Echinolittorina feejeensis* occurred on scattered granite rocks on sandy beaches in the splash zone of offshore islands where the water is clear both in the Gulf of Thailand and the Andaman Sea. It is dominant at Ko Kumpun, Trat Province. Altogether, there have now been 16 species of Littorinidae recorded in Thailand.

The two coasts of Thailand are both part of the vast Indo-West Pacific faunal region. While the Indo-West Pacific is considered to be a distinct biogeographical region, it is well known that there are some differences between the biota of the western Pacific Ocean and eastern Indian Ocean. Most mollusc species are widespread throughout the region. Wells (2002) studied distribution patterns of 1268 species of shallow water molluscs in the Indo-West Pacific, including littorinids. Diversity was higher (745 species) in the coral triangle, which included the Pacific coast of Thailand than in the eastern Indian Ocean (542 species), which included the Andaman Sea coast of Thailand. A small proportion (<6%) of the molluscs were restricted to one of the two areas. Recent studies (e.g. Benzie, 1999; Williams *et al.*, 2002) have shown that the distinction between Indian and Pacific Ocean populations also occurs at a genetic level within a single species. The reasons for the separation of the two areas are complex. At present the oceans are continuous, which allows at least some genetic exchange between the two areas. During Pleistocene periods of lower sea level the tropical portions of the two oceans were separated, allowing allopatric speciation to occur. The most recent period of lowered seawater was approximately 18,000 years ago, when sea levels were 130 m lower than now (Chappel and Shackleton, 1986).

The distribution of littorinids in Thailand fits into this general pattern. Most (10) of the littorinids found in the present study occurred on both coasts of Thailand, including all of the species of *Echinolittorina* and *Peasiella*, and most of the *Littoraria*. Four of the *Littoraria* (*L. bengalensis*, *L. conica*, *L. scabra*, and *L. undulata*) occurred only on the Andaman Sea side of the country. The known distribution of *L. bengalensis* is restricted to the Indian Ocean between India and Thailand (Reid, 1999). Reid (1986a) records *L. conica* and *L. scabra* from sites in the Pacific Ocean east of Thailand, and Rosewater (1970) presents similar data for *L. undulata*, and the species have been found in peninsular Malaysia. However, neither author records these species in the Gulf of Thailand. Granted the relatively few sites that had been examined in the Gulf of Thailand, the absence of records in the Gulf could have been real or an artefact of the lack of samples. The present study demonstrates the absence is real.

In most respects, the habitats occupied by *Littoraria* in Thailand are similar to those reported

by Reid (1985; 1986a, 2001b), though individual species in Thailand occur on mangroves from which they were previously not recorded. In fact, individual species were found on up to 14 different plant species. Reid (1985) showed that individual species are zoned on the shoreline. The present study demonstrates that the zonation is not specific to a particular type of tree, or necessarily even restricted to trees, but at the right tidal height species living in mangroves will inhabit a wide variety of trees. Some are also found on rocky or other wooden substrates, as noted by Reid (1986a). The main habitat difference that we found is a small proportion of several species, such as *L. strigata, L. articulata* and *L. melanostoma,* occurring on intertidal sand and mud among the mangroves, including the seaward pneumatophore zone. These animals were actively crawling between the pneumatophores and had not been dislodged from an overhanging part of the mangrove. Perhaps the presence of a small proportion of the populations on the mud surface is due to the moister conditions and heavier rainfall in Thailand compared with Townsville, Australia, where Reid (1986a) did most of his work. He also (Reid, 1985) worked in other areas, including two localities in Thailand, but did not find *Littoraria* on the mud surface in the other areas he examined.

Aside from *L. undulata,* all of the *Littoraria* species found in Thailand were mangrove species. Reid (1986a) reported that at least three of the *Littoraria* species living in mangroves are "oceanic" species which live in less turbid water than "continental" species which live in areas of greater turbidity. The "oceanic" species are *L. intermedia, L. pallescens* and *L. scabra.* The dendrogram (Figure 4) provides some support for this hypothesis. There is a clear grouping of rocky shore species comprised of the three species of *Echinolittorina,* one species of *Peasiella roepstorffiana* and *L. undulata.* Two of the three "oceanic" species (*L. intermedia* and *L. scabra*) have a loose association with the rocky shore species. The combination of rocky shore and mangrove habitats occupied by the two species allows them to live in both coastal and oceanic regions. However, the third "oceanic" species, *L. pallescens,* is clearly grouped with the *Littoraria* species found in mangroves, not with the rocky shore species. Examination of the distributional maps presented by Reid (1986a) indicates that the three "oceanic" species occur in the open water areas of the Pacific Ocean but also in the muddier waters of southeast Asia, including Thailand and the Malaysian peninsula. An alternative hypothesis is that diversity of *Littoraria* is greatest in the southeast Asian area, and decreases with increasing distance in all directions (east, west, north and south) in the Indo-Pacific. This parallels the general distributional pattern found in molluscs (e.g. Wells, 2002) and many other groups. In this context, the distributional patterns of *Littoraria* are consistent with the centre of biodiversity in the 'coral triangle', with lower diversity with increasing diversity from the central triangle rather than a division into "continental" and "oceanic" species.

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Appendix 1 Descriptions of sites examined for littorinids in Thailand.

Site 1. Yai Bay, Ko Kut, Ko Kut sub-amphur, Trat (11°36'37.5"N; 102°35'38.5"E) 5 Apr 2002. Rocky shore. *L. pallescens, L. strigata, E. feejeensis, E. trochoides, E. vidua, P. roepstorffiana.* **Site 2**. South of Ko Rad, Ko Kut sub-amphur, Trat (11°40'22"N; 102°31'35.5"E) 19 Nov 2001 Sandy beach with rocks. *L. strigata, E. feejeensis, E. trochoides, E. vidua.* **Site 3**. Hin Kongwaichaek, Ko Chang, Trat (11°57'21.2"N; 102°21'41.6"E). 18 Nov 2001 Rocky shore. *E. trochoides, E. vidua.* **Site 4**. Ko Krum, Ko Chang, Trat (11°55'1.7"N; 102°21'43.2"E) 18 Nov 2001 Rocky shore. *L. pallescens, E. trochoides.* **Site 5**. Ko Karm, Mak Is., Ko Chang, Trat (11°49'27.3"N; 102°27'48.2"E) 20 Nov 2001 Rocky shore. *E. trochoides, E. vidua.* Site 6. East of Ko Ra yungnork, Mak Is., Ko Chang, Trat (11°41'17.8"N; 102°27'16.6"E) 20 Nov 2001 Rocky shore. *E. trochoides, E. vidua.* **Site 7**. Ko Kumpun, Mak Is., Ko Chang, Trat (11°46'35.9"N; 102°21'48.6"E) 21 Nov 2001 Rocky shore. *E. feejeensis, E. trochoides, E. vidua.* **Site 8**. Ko Prao nok, Ko Chang, Trat (11°58'15.5"N; 102°23'47.5"E) 22 Nov 2001 Pier poles. *L. strigata.* **Site 9**. Ban Salukpet, Ko Chang, Trat (11°59'45.5"N; 102°22'32.5"E) 18–19 Nov 2001 A few *Avicennia marina* 2–3 m high and house poles. *L. pallescens, L. carinifera, L. strigata, L. articulata.* **Site 10**. Laem Hin, Ban Prednai, Moeng, Trat (12°9'48"N; 102°34'36.3"E) 17 Nov 2001 *Rhizophora apiculata* and *Avicennia alba* 5–7 m high and flat stones. *L. carinifera, L. pallescens, L. melanostoma.* **Site 11**. Ban Prednai mangrove, Moeng, Trat (12°7'38.9"N; 102°30'22.9"E) 7 Nov 2001 *Sonneratia griffithii, Avicennia alba, A. marina, Rhizophora apiculata, R. mucronata, Ceriops tagal, Bruguiera cylindrica,* and *Xylocarpus granatum* 5–10 m high. *L. pallescens, L. carinifera, L. strigata, L. articulata, L. melanostoma.* **Site 12**. Kung Kraben, Tamai, Chanthaburi (12°33'54.1"N; 101°54'9"E) 15 Dec 2002 Plantation area, with plants 1.5–4 m high, mostly *R. apiculata*, but also *R. mucronata, Lumnitzera racemosa, Ceriops decandra, C. tagal, A. alba, A. marina* and *Sonneratia alba*. *L. pallescens, L. carinifera, L. strigata, L. articulata, L. melanostoma.* **Site 13**. Tumbon Bankrum, Klaeng, Rayong (12°39'31.2"N; 101°39'52.3"E) 3 Dec 2001. Scattered *A. alba*, and some *R. apiculata* and *R. mucronata* and a small rock wall for protection from waves. *L. pallescens, L. carinifera, L. strigata, L. articulata, E. trochoides.* **Site 14**. Kord beach, Sattahip, Chonburi (12°41'45"N; 100°51'25.5"E). 29 Nov 2001 Scattered rocks. *E. trochoides, E. vidua.* **Site 15**. Krajong Bay, Ko Kram, Sattahip, Chonburi (12°41'15.5"N; 100°46'47.5"E) 26 Jan 2002 Rocky shore. *E. feejeensis, E. trochoides, E. vidua, P. roepstorffiana.* **Site 16**. Kam Bay, Ko Kram, Sattahip, Chonburi (12°41'9.8"N; 100°47'38.5"E) 27 January 2002 Scattered rocks. *E.. trochoides, E. vidua, P. roepstorffiana.* **Site 17**. Ko Yor, Sattahip, Chonburi (12°37'1.5"N; 100°53'7.5"E) 27 Jul 2002 Scattered rocks. *E. feejeensis, E. trochoides, E. vidua, P. roepstorffiana, L. strigata.* **Site 18**. Ko Larn, Pattaya, Chonburi (12°54'58.2"N; 100°46'19.4"E) 23 Feb 2002 Rocks. *E. trochoides, E. vidua, P. roepstorffiana.* **Site 19**. Koa Sammuk, Moeng, Chonburi (13°18'35.5"N; 100° 54' 21.4"E) 30 Oct 2002 Rocky shore. *L. strigata, L. articulata, E. trochoides.* **Site 20**. Bang Prong canal, Angsila, Moeng, Chonburi (13°18'33.8"N; 100°55'7.3"E) 30 Jul 2002 *A. marina, S. griffithii* and *Sesuvium portulacastrum*. *L. pallescens, L. strigata, L. articulata, L. melanostoma, L. carinifera.* **Site 21**. Samed, Moeng, Chonburi (13°20'21.2"N; 100°57'31.7"E) 4 Nov 2002 *A. alba* 4–7 m high. *L. strigata, L. articulata, L. melanostoma.* **Site 22**. Bangpu, Bangpu, Samut Prakarn (13°30'39.7"N; 100°38'56.2"E) 21Jul 2002 *A. marina* and *A. alba* 3–7 m high and rocks. *L. strigata, L. articulata, L. melanostoma.* **Site 23**. Had, Laemloung, T.Laempukbia, Banlaem, Phetchaburi (13°2'13.4"N; 100°5'50.3"E) 14 Dec 2002 *R. apiculata, R. mucronata,* and *A. alba* 7–10 m high. *L. strigata, L. articulata, L. melanostoma, L. carinifera.* **Site 24**. PTT mangrove, T. Paknampran, Pranburi, Prachuap Khiri Khan (12°23'17.5"N; 99°59'2.3"E) 9 Dec 2002 *A. marina, R. mucronata,* and *R. apiculata* 3–4 m high. *L. strigata, L. articulata, L. melanostoma, L. carinifera.* **Site 25**. E–led canal, Chumphon Islands Marine Park, Chumphon (10°21'1.2"N; 99°14'2.1"E) 24 Dec 2001 *R. apiculata* and *R.. mucronata* 15 m high, but some planted areas 1.5 m high. *L. strigata, L. articulata, L. melanostoma, L. carinifera, L. pallescens.* **Site 26**. Ban Cha-ngoe, Tumbon Takienthong, Kanjanadit, Surat Thani (12°40'53.9"N; 100°46'38.7"E) 3 Dec 2002. *R. apiculata* mixed with *A. marina*. *R. mucronata* and *S. alba* 5–15 m high. *L. strigata, L. articulata, L. melanostoma.* **Site 27**. Don Sak Ferry, Don Sak, Surat Thani (9°19'55.7"N; 99°41'28.5"E) 19 Dec 2001 Rocks. *L. strigata, L. articulata, E. trochoides.* **Site 28**. Ban Taling ngam, Ko Samui, Surat Thani (9°42'47"N; 99°58'33.7"E) 22 Dec 2001 Granite rocks. *L. strigata, L. articulata, E. trochoides.* **Site 29**. Ko Kor Ma, Ko Pangun, Surat Thani (9°47'27"N; 99°58'52.8"E) 21 Dec 2001 Scattered rocks. *L. strigata, L. articulata, E. trochoides, E. vidua.* **Site 30** Laem Yai, Ko Samui, Surat Thani (9°33'50.6"N; 99°55'6.9"E) 20 Dec 2001 Rocky shore. *L. strigata, L. articulata, E. trochoides, E. vidua, E. feejeensis.* **Site 31**. Hin Ta Hin Yai, Ko Samui Surat Thani 22 Dec 2001 (9°27'3.7"N; 100°2'37.5"E) Scattered granite rocks. *L. strigata, L. articulata, E. trochoides.* **Site 32**. Tumbon Pak Nakorn, Moeng, Nakhon Si Thammarat (8°28'7.8"N; 100°3'52.9"E) 28 Aug 2002 *R. mucronata, A. alba* and *A. marina* 2–4 m high. *L. strigata, L. articulata, L. melanostoma, L. pallescens.* **Site 33** Pak Panung Bay, Pak Panung, Nakhon Si Thammarat (8°23'40.7"N; 100°10'18.5"E) 27 Aug 2002. Mouth of Pak Panung canal. Mostly *R. apiculata,* and *R. mucronata* 5–15 m high. *L. melanostoma.* **Site 34**. Ban Laem Tachi, Yaring, Pattani (6°55'40.8"N; 101°14'38.0"E) 13 Oct 2002 Rock seawall. *L. strigata.* **Site 35**. Ban Dee, Yaring, Pattani (6°55'15.5"N; 101°19'35.5"E) 13 Oct 2002 *R. mucronata* 5 m high in Pattani Bay. *L. pallescens.* **Site 36**. Ban Da To, Yaring, Pattani (6°54'18.4"N; 101°20'19.2"E) 13 Oct 2002 A. marina 4–5 m high, Pattani Bay. *L. strigata, L. melanostoma, L. carinifera, L. intermedia.* **Site 37**. KaeKae Beach,Tumbon Nambo, Panarei, Pattani (6°50'16.3"N; 101°33'28.9"E) 4 Dec 2002 Scattered rocks. *E. trochoides.* **Site 38**. Naratat Beach, Moeng, Narathiwat (6°26'32.5"N; 101°49'18.6"E) 4 Dec 2002 Small *L. racemosa* and *Nypa fruticans*. *L. carinifera, L. pallescens.* **Site 39**. Ban Je Bilung, Je Bilung, Satun (6°38'21.2"N; 99°58'3.8"E) 5 Dec 2002. *R. apiculata* and *R. mucronata* 5–10 m. *L. carinifera, Littoraria conica, L. bengalensis, L. melanostoma.* **Site 40**. Petra Is. Nat.Park,Tumbon Pakbara, Langu, Satun (6°49'43"N; 99°45'31.1"E) 5 Dec 2002 Scattered *A. marina* 3–4 m high. *L. strigata.* **Site 41**. Chaomai Beach, Kun Tung, Trang (7°18'5.5"N; (99°24'19.1"E) 31 Aug 2002 *A. alba, A. marina,* and *S. griffithii*. *L. pallescens, L. strigata, L. intermedia, L. bengalensis, L. scabra, E. trochoides.* **Site 42**. Pak Meng Beach, Tumbon Ko Libong, Kun Tung, Trang (7°27'37.6"N; 99°20'23.6"E) 6 Dec 2002 *A. marina* 3–5m high. *L. carinifera, L. bengalensis, L. strigata.* **Site 43**. Shell cemetery,Tumbon Saithai, Moeng, Krabi (8°00'53.2"N; 98°53'11.8"E) 6 Dec 2002 Rocky shore and dead wood. *L.*

strigata, E. trochoides. **Site 44.** Ta la Beach, Tumbon Ban pa klok, Talang, Phuket (8°1'10.8"N; 98°24'51.2"E) 7 Dec 2002 *A. marina, R. mucronata,* and *S. griffithii* 5–7 m high. *L. pallescens, L. strigata, L. bengalensis.* **Site 45.** Kalim Beach, Kratu, Phuket (7°54'11"N; 98°17'53.6"E) 7 Dec 2002 Scattered rocks. *L. undulata, E. trochoides, E. vidua, E. feejeensis.* **Site 46.** Mai ngarm Bay, Ko North Surin, Phangnga (9°26'27.7"N; 97°52'48.5"E) 20 Apr 2002 Rocky shore with scattered *R. apiculata* and *R. mucronata. E. trochoides, E. vidua, P. roepstorffiana, L. undulata, L. intermedia, L. scabra, L. pallescens.* **Site 47.** Ko Jong, Kuraburi, Phangnga (9°13'12.5"N; 98°20'55.7"E) 2 Sep 2002 *A. marina, R. mucronata,* and *S. griffithii. L. scabra, L. strigata, L. bengalensis, L. pallescens, E. vidua, E. trochoides.* **Site 48.** Ko Ra, Kuraburi, Phangnga (9°15'21.5"N; 98°22'30.5"E) 2 Sep 2002 Rocky shore. *E. trochoides, E. vidua, P. roepstorffiana, L. undulata, L. strigata.* **Site 49.** Laem Mai Kaew, Ban Ta lei nok, Tumbon Naka, Suksumran sub-amphur, Ranong (9°27'58.5"N; 98°26'13.9"E) 3 Sep 2002 *Finlaysonia maritima, C. decandra* and *Aegialites rotundifolia. L. carinifera, L. melanostoma, L. bengalensis, L. conica, L. pallescens.* **Site 50.** Klong Kone, Tumbon Klong Kone, Moeng, Samut Songkram (13°19'34.5"N; 99°58'30"E) August 2003. *Sonneratia caseolaris,* 5–10 m high. *L. articulata, L. strigata, L. melanostoma.*

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